Canid evolution and palaeoecology in the Pleistocene of western Europe, with particular reference to the wolf *Canis lupus* L. 1758.

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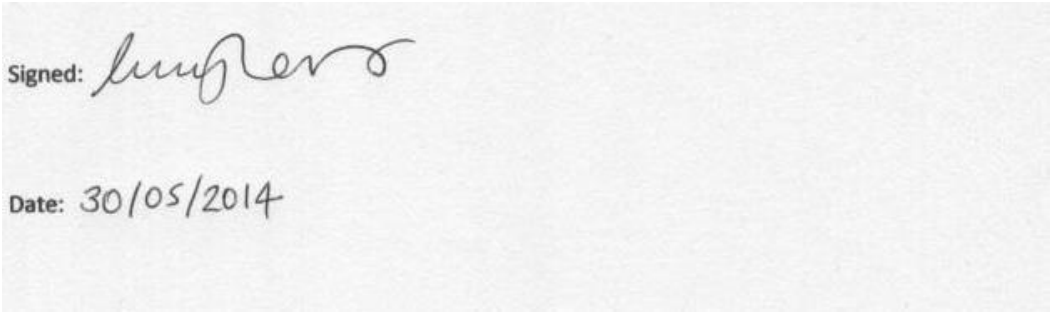
Declaration of Authorship

I, Lucy Olivia Holman Flower, hereby declare that this thesis and the work presented in it is entirely my own. Where I have consulted the work of others, this is always clearly stated.



Abstract

The palaeoecology of a range of Pleistocene canids (*Canis etruscus, Canis arnensis, Canis mosbachensis* and *Canis lupus*) was investigated from sites in Britain and mainland Europe. Based on detailed morphometric data, including a suite of dietary-diagnostic cranio-dental measurements, estimates of body mass were made, and palaeodiet examined to elucidate within-species temporal, climatic and regional dietary differences, as well as inter-species palaeodietary differences. Tooth breakage and level of wear were also analysed to further reveal temporal dietary differences.

A lack of temporal variability in the diets of *C. etruscus* and *C. mosbachensis* is linked here to the relative climatic stability in the Early Pleistocene, associated with a diverse and abundant prey base. The large and species-rich carnivore community of this period constrained the body sizes and prey choices of these canids, in particular competition from larger canids.

In contrast, the diet of *C. lupus* showed much greater temporal variation, likely reflecting the dramatic climatic changes of the late Middle and Late Pleistocene, which led to differences in the openness of the environment as well as changes in large carnivore competition. Body size was also more variable within Pleistocene wolves, with an increasing size trend evident during the Devensian, although within range of their modern counterparts. The flexible and adaptive ecology of *C. lupus* was thus apparently the key to its tenacity as a species throughout the later Pleistocene and into modern times.

Finally, based on morphological, morphometrical and palaeoecological inferences, the wolf evolutionary lineage was examined. Both *C. etruscus* and *C. mosbachensis* were considered to be members of the early wolf lineage, whereas *C. lupus* may have had a separate origination and subsequent dispersal into western Europe. *C. mosbachensis* was not considered here to be a subspecies of *C. lupus* due to the overall lack of similarity between the species.

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1. Introduction

This research explores body size and palaeoecology in Pleistocene canids, with particular reference to *Canis etruscus, Canis arnensis, Canis mosbachensis* and *Canis lupus*. Body size and ecology are highly interrelated and underpin a large range of factors in carnivores, including life history traits, prey choice and competitive interactions. Thus, any changes in them may have far reaching consequences for the rest of the mammalian community.

1.1. Extant *Canis lupus* as a modern ecological analogue

Modern *C. lupus* can be used as an analogue for Pleistocene canids, informing about morphology and adaptations, ecology and competition. Today, the wolf is the largest member of the Family Canidae (Mech, 1970; Stains, 1975; Macdonald, 2009) and is an intelligent, highly social and cooperative predator that is well adapted to its environment and mode of life. In terms of adaptations, its cranio-dental morphology characterises its hypercarnivorous yet generalist diet, and its limbs are modified for a cursorial habit (Mech, 1970).

Although the Pleistocene *C. lupus* was one of the most abundant and widely distributed mammals in the Palaearctic, its modern range is comparatively much reduced. Populations today inhabit wild and remote areas of northern North America, northern Asia, and parts of Europe (Mech and Boitani, 2010). *C. lupus* is regionally extinct in much of western Europe, although the increased protection of remnant wolf populations, natural recolonisation and more progressive attitudes towards large carnivore conservation are encouraging for western European wolf recovery.

In Britain, wolves were extirpated by the 18th Century (Bueler, 1973). There is, however, ongoing debate regarding re-introduction of wolves as a keystone predator into the Scottish Highlands (for a detailed summary see Manning *et al*., 2009), which would re-balance the regional ecology by regulating excessive numbers of red deer (*Cervus elaphus*). The prospect of 're-wilding' using extirpated native species is fraught with controversy but may yet prove the salvation of the wolf.

As a social carnivore, *C. lupus* lives in packs, representing a group of wolves with bonds of association, hunting and resting together (Mech, 1970). Generally, this comprises a breeding pair and their offspring but can also contain several adults of breeding condition (Mech, 1970). Today in the Palaearctic, wolves are the only large remaining pursuit

predator, defined as animals that chase their prey for a distance of greater than 300m (Ewer, 1973). Their cursorial adaptation, combined with their cooperative hunting behaviour, enable them to capture and kill prey much larger than themselves (Macdonald, 1983). Typically, this involves (frequently extended) pursuit and subsequent attack by tearing flesh from the hindquarters and shoulders (Ewer, 1973; Mech, 1970). Prey selection is deliberate, based on species, age and sex and potential risk of injury (Stahler *et al.,* 2006). Feeding commences immediately after the kill, with flesh on the flanks consumed quickly and rapid access gained the viscera (Mech, 1970). Carcass utilisation varies according to competition and ease of hunting; carcasses are more fully utilised when hunting is difficult (Mech *et al.,* 1971) as opposed to when prey is readily abundant (Haynes, 1982).

The diet of *C. lupus* has been extensively documented. Case studies from North America (Voigt *et al*., 1976; Fritts and Mech, 1981; Paquet, 1992; Boyd *et al*., 1994) and Europe (Jędrzejewski *et al.,* 2000; Kojola *et al*., 2004; Capitani *et al*., 2003; Ansorge *et al*., 2006; Nowak *et al*., 2011) reveal ungulate prey to be the focus. In North America, white-tailed deer (*Odocoileus virginianus*), elk (*Cervus canadensis*) and moose (*Alces alces*) are favoured, whereas red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) are targeted in Europe, along with reindeer at high latitudes.

Where availability of wild ungulates is permanently or seasonally low, *C. lupus* adapts by hunting smaller vertebrates, such as North American beaver (*Castor canadensis*) (Voigt *et al*., 1976), and in Europe, Eurasian beaver (*Castor fiber*), leporids and birds (Jędrzejewski *et al*., 2000). Scarcity of wild ungulates can also increase predation on livestock (Meriggi and Lovari, 1996; Vos, 2000), as well as consumption of household waste (Pullianen, 1975; Rogers and Mech, 1981), both leading to conflict with humans.

The nature of the human-wolf relationship is an important factor in the story of *C. lupus*. Competition for food, hunting ranges and habitat have long been a cause of rivalry (Bueler, 1973; Pullianen, 1975), continuing today through predation of domestic livestock (Wabakken *et al*., 2001). In contrast, more positive examples of relationships exist, including the reverential treatment of animals at the early Neolithic wolf burial at Lokomotiv-Raisovet, Siberia (see Losey *et al*., 2011) and ultimately, the domestication of *C. lupus* as dogs (Clutton Brock, 1995; Vila *et al*., 1997).

According to archaeological evidence (see Deguilloux *et al*., 2009 and Germonpré *et al*., 2009 for reviews), the oldest known domestic dog remains include a humerus from Erralla, Spain dated to 16,000-12,500 years BP (Vigne, 2005), a young dog buried with a human in

Israel dated to 12,000-11,000 years ago (Davis and Valla, 1978) and remains from Eliseevichi I, Russia, dated to 17,000-13,000 ^{14}C years BP (Sablin and Klopachev, 2002).

Nevertheless, using archaeological evidence to pinpoint the timing of domestication is both difficult and controversial (Larson *et al*., 2012). Although the majority of well documented remains are from the Late Glacial, tentative evidence exists for earlier possible forays into domestication, including large 'dogs' from Razboinichya Cave in southern Siberia, dated to c.33,000 cal BP. (Ovodov *et al*., 2011) and from Goyet, Belgium, dated to ~31,700 BP (Germonpré *et al*., 2009), although both finds are controversial. Crockford and Kuzmin (2012) suggested that these specimens instead represent wolves that adapted due to Palaeolithic human competition, rather than indicating morphological evidence for domestication.

Based on genetic evidence, dog-wolf divergence has been estimated at ~15, 000 yr BP (Savolainen *et al*., 2002), as well as up to ~30,000 years BP when modelled on a low rate of gene flow (Skoglund *et al*., 2011). Both estimates indicate a likely Asian origin for domestication, in particular East Asia (Savolainen *et al*., 2002) and southern Asia (Skoglund *et al*., 2011). However, the exact timing, location and number of founder wolf populations remain unclear. Part of the problem is the subsequent merging and homogenisation of multiple independent dog lineages over time, which led to increased gene flow, ultimately obscuring the origins of domestication (Larson *et al*., 2012).

The wolf is therefore an integral component of present and past ecosystems, acting as a regulator of large ungulates and thus promoting greater biodiversity, as well as being highly adaptable in the face of environmental and biotic change. As well as modern *C. lupus*, the morphology, body mass, ecology and feeding behaviour of other living canids, such as wild dog *Lycaon pictus* and dhole *Cuon alpinus*, can be used as analogues to infer past community structure and competitive interactions amongst different Pleistocene canids.

1.2. Research aims

The overarching research aim is to use detailed morphometric data and estimation of body mass in order to elucidate the palaeoecology and lineage relationships of European Pleistocene canids, and especially, British Pleistocene wolves.

For the species studies (*C. etruscus, C. arnensis, C. mosbachensis* and *C. lupus*) comparisons, wherever possible, will be made temporally (from the first appearance of the wolf-like *C.*

etruscus in Europe c.2.2 Ma to the end of the Pleistocene) within-species, between species and finally, with extant canids. Material from Britain, Germany and Italy will be the focus of the research, allowing change across a geographical transect from western to central to southern Europe to be addressed.

It is anticipated that the combination of temporal and regional information will elucidate palaeoclimatic impacts on the different canids and their responses to changing palaeoenvironments. Furthermore, comparisons between the Pleistocene species, as well as with extant canids, will highlight potential differences in palaeoecology and palaeodiet, allowing prey choice and competitive interactions to be reconstructed. Finally, inferences regarding the lineage of the wolf-like canids may be possible, especially the phylogenetic position of *C. mosbachensis* as a subspecies of *C. lupus* or as a separate species.

The research will therefore target three key questions:

1). How and why did canid body mass change over the Pleistocene?

The estimation of body mass, used as a surrogate for body size, will reveal basic ecological parameters for the Pleistocene species, such as prey choice and position in the carnivore guild, as well as examining any correlation with climatic or environmental change.

2). How and why did canid ecology change over the Pleistocene?

The proportions of flesh, bone and non-flesh foods in the palaeodiet of Pleistocene canids will be inferred from cranio-dental measurements, thus revealing the relative degree of carnivory or omnivory. It is anticipated that interspecific variations in palaeodiet will elucidate the ecological niches of the different canids involved. Any variation in palaeodiet within and between species, combined with body mass evidence, will then be examined against changes in carnivore guild, and climatic and environmental parameters to establish forcing factors.

3). How did the wolf lineage evolve in Europe?

Inferences regarding the phylogenetic relationships of the wolf-like canids will incorporate evidence from the previous two questions, combined with detailed morphological information. The phylogenetic position of *C. mosbachensis* will also be examined based on the above findings.

2. Background and rationale

The following chapter is divided into three sections. The first introduces the origin and dispersal of members of the genus *Canis* during the Plio-Pleistocene, setting the scene for the four canids of interest to this research: *Canis etruscus, Canis arnensis, Canis mosbachensis* and *C. lupus*. The second section examines the origin and development of cursoriality and social behaviour in canids, as well as outlining the cranio-dental adaptations relating to hunting in modern *C. lupus*, as an analogue for the Pleistocene canids. The final section describes and compares the morphology of the four study species, as well as presenting the lineage relationships between these canids and briefly, from other contemporary species of Pleistocene canid.

2.1.1. The first occurrence of *Canis*

The genus *Canis* is first recognised in North America in the late Hemphillian (North American Land Mammal Stage) at the Miocene-Pliocene boundary, around 5.5 Ma (Masini and Torre, 1990; Rook and Torre, 1996a; Rook *et al.,* 2007; Wang and Tedford, 2007).

The earliest member of *Canis* was originally thought to be *Canis davisi* Merriam, 1911 (Van Valkenburgh, 1988a; Rook and Torre, 1996a). However, *C. davisi* appears less derived in comparison to other members of *Canis*, because of the absence of a transverse cristid connecting the hypoconid and entoconid of the m1 talonid, a characteristic feature of the Caninae (Tedford and Qui, 1996). It was subsequently removed from the genus *Canis* (Berta, 1987) and incorporated into the genus *Eucyon* by Tedford and Qui (1996) as *Eucyon davisi* (Merriam, 1911), representing the founder member of this genus. More recently, *Canis lepophagus* Johnston, 1938, has been proposed as the earliest member of *Canis* and has been phylogenetically linked to the modern coyote, *Canis latrans* Say, 1823 (Garrido and Arribas, 2008). *Canis ferox* Miller and Carranza-Castaneda, 1998 also appeared during the North American early Pliocene (Wang and Tedford, 2007).

Nevertheless, the geographical whereabouts of the origins of *Canis* remain controversial. In Europe, fragmentary remains were originally attributed to a medium-sized *Canis* at Concud (=Cerro della Gariata) (Torre, 1979) and Los Mansuetos, both in Spain (Sotnikova and Rook, 2010), dating to the end Turolian (Miocene, 9-5.3 Ma). This canid was identified as the oldest representative of '*Canis*' *cipio*, although its phylogenetic position and possible ancestry are uncertain, since the remains are too fragmentary for further diagnosis

(Sotnikova and Rook, 2010). Wang and Tedford (2007), in contrast, considered *C. cipio* to be a member of *Eucyon* rather than a true species of *Canis*, whereas Garrido and Arribas (2008) related it to *Canis michauxi* Martin, 1973 from the early Pliocene of France. Interestingly, both *C. michauxi* and *C. cipio* were thought to be related to the later *C. etruscus* (Torre, 1979; Rook, 1992). *C. michauxi* is only known from two mandibular fragments, both now apparently lost, although previously-recorded metrical data indicate a large canid with a p3 larger and deeper than found in *Eucyon* (Spassov and Rook, 2006).

Unfortunately, the remains of both species are too few to make a reliable generic determination and comparison (Rook, 1992; Spassov and Rook, 2006). Garrido and Arribas (2008) tentatively believed that *C. cipio* should remain classified with *Canis*. However, if both *C. cipio* and *C. michauxi* are *Eucyon,* they are the largest members of the genus (Rook, 1992; Montoya *et al.,* 2009). Doubts over the identification of early *Canis* (see Masini and Torre, 1990) also rest on the perceived absence of the *Canis* genus during the Early and Middle Villafranchian in Western Europe (Azzaroli, 1983; Azzaroli *et al.,* 1988), which will be returned to later.

An alternative Asian origin for the genus *Canis* has also been suggested (see Sardella and Palombo, 2007), based on records from the Mazegu Formation, Yushe Basin, China dated to 3.4-3 Ma (late Pliocene) (Flynn *et al.,* 1991; Sotnikova *et al.,* 2002; Sardella and Palombo, 2007). The Yushe *Canis* has anatomical characteristics similar to those of the late Villafranchian *Canis etruscus* Forsyth Major, 1877 (Garrido and Arribas, 2008) but (as a further complication), it has also been compared to *Eucyon* (Sardella and Palombo, 2007), which radiated into Asia around the same time as *Canis* and is similar in both morphology and size (Sardella and Palombo, 2007). However, if a North American origin is accepted, the earliest dispersal of *Canis* across the Bering Strait into Asia had occurred by at least the early Pliocene (Rook and Torre, 1996a; Garrido and Arribas, 2008). Instead of having an Asian origin, *Canis* might thus simply be a long-distance immigrant into the Yushe region (Flynn *et al.,* 1991).

The divided opinions above highlight the problems with the record, chiefly misidentification of species due to similar morphology between *Canis* (especially the wolf group) and *Eucyon* (Sardella and Palombo, 2007; Garrido and Arribas, 2008), for example the presence of a second posterior cusplet on the p4 (Tedford and Qui, 1996). The evolutionary history of the genus *Canis* thus remains obscure in some aspects, with both its geographical origins

and the timing of its dispersal into Eurasia remaining the subject of investigation (Rook *et al.,* 2007).

2.1.2. Dispersal into Europe and problems with the record

Nonetheless, it is clear that *Canis* migrated into Europe from Asia (Sotnikova *et al.,* 2002). At the Pliocene locality of Kuruksai in Tajikistan, dated to 2.5 Ma, a jackal-like canid, *Canis kuruksaensis* Sotnikova, 1989, is recorded (Rook and Torre, 1996a). Originally, it was thought to represent the earliest Asian *Canis* recorded in the European Middle Villafranchian (Sotnikova *et al.,* 2002) but again, there are difficulties in determining whether this species belongs to *Canis* or *Eucyon.* Whereas Sardella and Palombo (2007) favoured *C. kuruksaensis* as a late form of *Eucyon*, Sotnikova and Rook (2010) proposed that although in some aspects it conforms to *Eucyon*, it is more morphologically advanced in the direction of *Canis*.

C. kuruksaensis retains the less derived characteristics of *Eucyon*, such as the fan-shaped supraoccipital shield and the absence of a transverse cristid uniting the m1 entoconid and hypoconid (Sotnikova and Rook, 2010). However, it differs significantly from *Eucyon* in its larger teeth, its longer P4-M1 row, and by the presence of a transversely-extended M1 with a taller paracone and metacone, including a more developed parastyle and a cusp-like metaconule, with a concave outline of the labial cingulum (Sotnikova and Rook, 2010). These features are more similar to *Canis* and Sotnikova and Rook (2010) concluded by retaining the name *'Canis' kuruksaensis*, using inverted commas to denote the unresolved difficulties in the identification.

As well as the early *Canis* forms of *C. cipio* and *C. michauxi* in the early Pliocene, other canid fossils attributed to *Canis adoxus* Martin, 1973 and *Canis odessanus* Odintzov, 1967 have been found in southern and eastern Europe respectively (Masini and Torre, 1990; Rook and Torre, 1996a; Spassov and Rook, 2006) and were believed to be closely related to the aforementioned Yushe finds from China (Rook and Torre, 1996a). In Europe, *C. adoxus* has been recorded at St Estève, France, and Torre (1979) initially proposed close affinity with the *Canis* sp. identified from Venta del Moro, Spain (Torre, 1979). However, the latter was subsequently reassigned to *Eucyon*, as *Eucyon monticinensis* (Rook, 1992) by Garrido and Arribas (2008), although differences had been identified by Rook (1992) between *C. adoxus* and *E. monticinensis*, namely the larger size, elongate muzzle and reduced premolars of the former.

A review of *C. adoxus* showed that it displayed the typical morphology and substantially smaller dimensions of *Eucyon* rather than *Canis* (Rook and Torre, 1996a; Spassov and Rook, 2006; Garrido and Arribas, 2008), close in size to *Eucyon zhoui* Tedford and Qui, 1996 and smaller than *C. lepophagus* (Sotnikova and Rook, 2010). Although it was a more advanced form than the Miocene-Pliocene *Eucyon*, it was not as derived as *Canis* (Sotnikova and Rook, 2010). In addition, some of its derived dental features are synapomorphies for other canine lineages and Tedford and Qui (1996) therefore suggested that it could represent a taxon other than *Eucyon*. Hence, the position of *C. adoxus* remains uncertain. *C. odessanus* was a very large canid from the Odessa Catacombs, Ukraine (Spassov and Rook, 2006). Its less derived characteristics invited comparison with *Eucyon* (Rook and Torre, 1996a) and it was renamed *Eucyon odessanus* (Odinzow, 1967) by Garrido and Arribas (2008). Spassov and Rook (2006) considered the teeth of *E. odessanus* to be distinct from, but of similar dimensions to the early *E. davisi,* although with a shorter and deeper p3 and both p3 and p4 being more variable and more conical.

Again, difficulties with identification hamper understanding of the origins and dispersal of *Canis* into Europe and none of the above taxa can definitively be attributed to *Canis*. The overall homogeneity between members of *Canis* (Garrido and Arribas, 2008) makes distinction between certain fossil species, and even between related genera difficult. As can be seen in this review, it is also further complicated by the multitude of *Canis* and *Eucyon* species described and their wide geographical distribution.

2.1.3. The chronology of *Canis* evolution in Europe

The following section introduces the chronology of *Canis* evolution in Europe during the Pliocene and Pleistocene. Following the majority of published reviews on their evolution, European Land Mammal Ages will be used as a time frame, which subdivide the stratigraphical stages in Europe.

The Ruscinian (5.3-3.5 Ma) corresponds to the Early Pliocene (Zanclean stage), whilst the Villafranchian (3.5-1.0 Ma) corresponds to the Late Pliocene (Piacenzian stage) to Early Pleistocene. The Villafranchian is a biochronological unit based on European large mammals, and is split into Early, Middle and Late, succeeded by the Galerian, which represents the early Middle Pleistocene (Azzaroli *et al.,* 1988), and the Aurelian the rest of the Pleistocene. Following the 2009 recommendations of the International Union of Geological Sciences, the base of the Pleistocene (and thus the Quaternary) was lowered to

incorporate the Galesian (2.588-1.806 Ma, formerly Late Pliocene). In light of this, the Early Villafranchian therefore now covers the Late Pliocene (~3.5 to 2.58 Ma, formerly the Mid Pliocene), the Middle Villafranchian represents the early part of the Early Pleistocene (~2.6 to 2.0 Ma, formerly most of the Late Pliocene), and the Late Villafranchian covers the remaining Early Pleistocene (~2.0 to 1.0 Ma, formerly latest part of late Pliocene to most of early Pleistocene) (Rook and Martinez-Navarro, 2010).

In Italy, Faunal Units further subdivide the Land Mammal Ages, which are based on faunal turnover (Rook *et al.,* 2007). For the Early Villafranchian, the Triversa F.U. and the Montopoli F.U. represent the early and late Early Villafranchian respectively. However, there are no definitive Middle Villafranchian F.Us identified. The Olivola F.U. marks the beginning of the Late Villafranchian, and is followed by the Tasso F.U., although the remaining Late Villafranchian assemblages are poorly known. Although the term 'Villafranchian' has lost its intrinsic value, its use is continued for stability in the literature, although it has no meaning unless used with Early, Middle or Late, or with a corresponding faunal unit (Rook and Martinez-Navarro, 2010). However, problems exist with correlation, particularly with the marine oxygen isotope record (MIS). Figure 2.1 illustrates the chronostratigraphy of key sites mentioned in the text from Britain and Europe, showing the range of *C. etruscus, C. arnensis, C. mosbachensis* and *C. lupus*, as well as *Canis falconeri* and *Canis* (*Xenocyon*) *lycaonoides*.

2.1.3.1. The Early Villafranchian record

Previously *Canis* was believed to have 'disappeared' from Europe in the Early Villafranchian, returning only at the beginning of the Late Villafranchian from an Asian refugium (Azzaroli *et al.* 1988). However, it seems unlikely that all members of *Canis* left Europe, since the oldest uncontroversial remains of *Canis* come from Vialette (Haute-Loire, southern France), correlated with the Triversa F.U. in the Early Villafranchian by magnetostratigraphy (Lacombat *et al.,* 2008), and confirmed by a fission track age of 3.14±0.6 Ma (Thouveny and Bonifay, 1984).

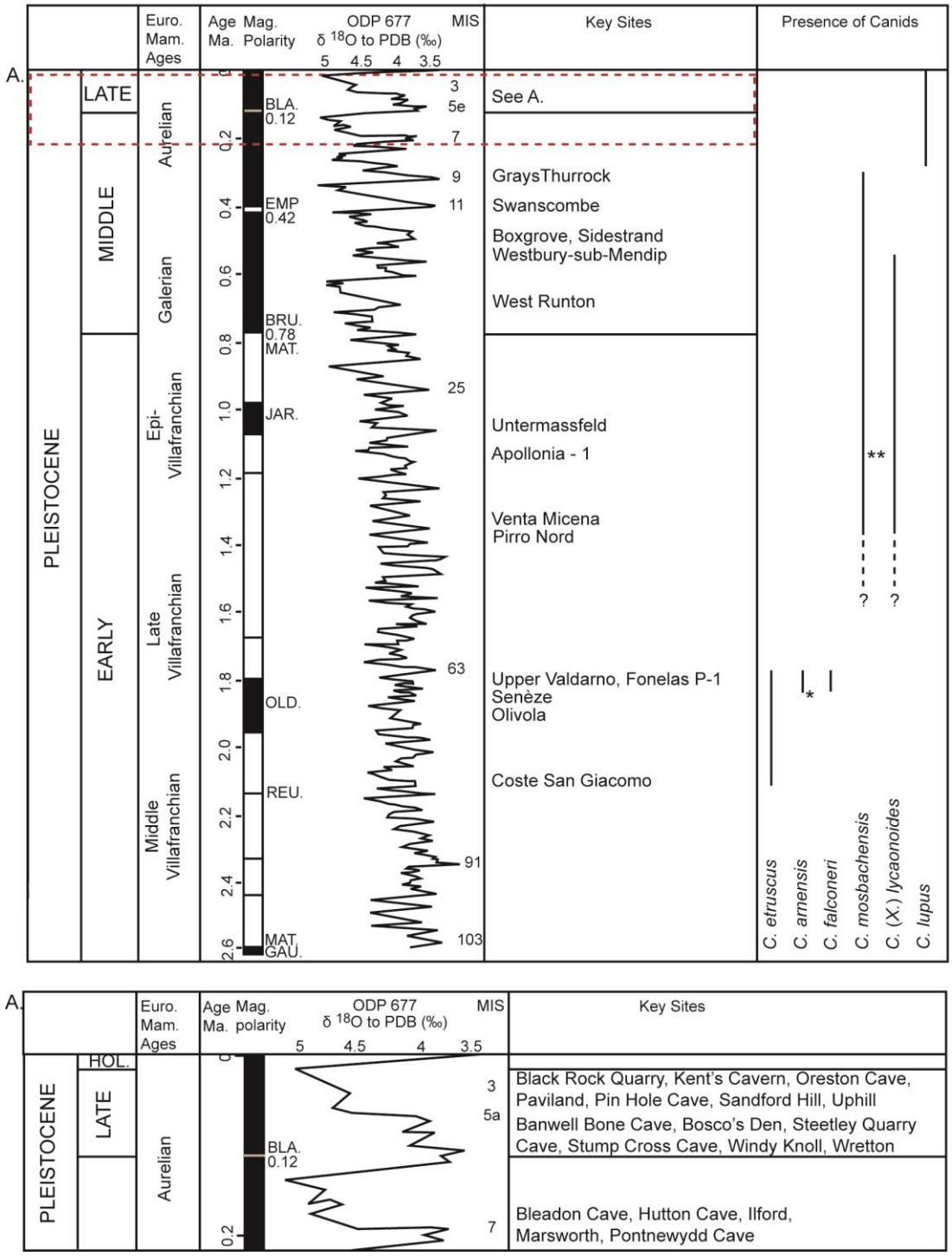


Figure 2.1. Chronostratigraphy of indicative sites (2.6 Ma to the present) from Europe mentioned in the text, and the chronological range of key canids. **A**: Detailed view of the chronostratigraphy of indicative sites of the late Middle to Late Pleistocene from Britain. Uncertainties with taxonomic status indicated by * for *C. senezensis* = *C. arnensis*, ** for *C. apolloniensis* = *C. mosbachensis*. Age, magnetic polarity and oxygen isotope calibration from Shackleton et al. (1990).

The Vialette remains were assigned to *Canis* as the morphology, size and proportions were not characteristic of *Eucyon*, although a species was not allocated (Lacombat *et al*., 2008). However, Lacombat et al. (2008) furthermore considered this to be an isolated appearance of *Canis* in the Early Villafranchian, noting that occurrences in the Middle Villafranchian were more numerous.

2.1.3.2. The Middle Villafranchian record

In Eastern Europe, the Khapry and Liventsovka faunal assemblages from Russia have been correlated with the central and western European Middle Villafranchian (Sotnikova *et al.,* 2002; Kahlke *et al*., 2011). Both sites contain canid remains attributed to *Canis senezensis* Martin, 1973, a species recognised from the Late Villafranchian (Sardella and Palombo, 2007; Sotnikova and Rook, 2010), although this identification was not without caution (Sotnikova *et al.,* 2002; Sotnikova and Rook, 2010). Interestingly the wide and short talonid of the m1 in the Khapry wolf was also considered similar to that of the earlier *'Canis' kuruksaensis* (Sotnikova and Rook, 2010), itself of controversial attribution to *Canis*. In western Europe, other early *Canis* remains at the Middle Villafranchian site of Coste San Giacomo, Italy, dated to 2.2-2.1 Ma, have been assigned *Canis* cf. *etruscus*, and represent the earliest remains of this classically Late Villafranchian species (Rook and Torre, 1996a; Sardella and Palombo, 2007; Rook and Martinez-Navarro, 2010).

The presence of canids during the Early and Middle Villafranchian is significant as it confirms that members of the genus did not completely disappear from Europe (*contra* Azzaroli, 1983; Azzaroli *et al.,* 1988). The presence of these early European canids also questions the timing of the so called Late Villafranchian 'Wolf Event', which traditionally marks the expansion of *Canis* in western Europe (see later). Although the Khapry *Canis* cf. s*enezensis* may indicate an early dispersal of *Canis* in eastern Europe (Sotnikova *et al.,* 2002), the sporadic finds of Early and Middle Villafranchian canids in France and Italy suggest that perhaps small populations reached western Europe prior to this, with widespread radiation only occurring at the onset of the Late Villafranchian (Rook and Torre, 1996a; Sardella and Palombo, 2007; Lacombat *et al*., 2008).

2.1.3.3. The Late Villafranchian and the 'Wolf Event'

The transition from the Middle to Late Villafranchian is traditionally marked by the so-called 'Wolf Event', originally recognised by Azzaroli (1983) at the late Villafranchian type site of the Olivola F.U. at Val di Magra, Italy. At the typesite, the transition between the Olivola F.U. and the succeeding Tasso F.U. is correlated with the top of the Olduvai palaeomagnetic subchron (Napoleone *et al*., 2003), suggesting an age slightly older than 1.8Ma. This event signified a pronounced faunal change from the Middle Villafranchian (Azzaroli, 1983; Azzaroli *et al.* 1988) and heralded the widespread expansion into Europe of the early 'wolf' *Canis etruscus* (Azzaroli, 1983; Azzaroli *et al.* 1988; Masini and Torre, 1990; Gliozzi *et al.,* 1997; Rook *et al.,* 2007), as well as the expansion of *Pachycrocuta brevirostris, Panthera gombaszoegensis* and the bovine *Leptobos etruscus* (Azzaroli *et al.* 1988). The event also witnessed the disappearance of species such as *Leptobos stenometopon, Procapreolus suanus, Sus minor, Ursus minimus* and various viverrids amongst others (Azzaroli *et al.* 1988; Kahlke *et al*., 2011). However, as discussed above, the expansion of *C. etruscus* into Europe is now considered to have occurred earlier, in the Middle Villafranchian.

The succeeding Tasso F.U. in Italy contained similar elements to the Olivola F.U. (Azzaroli *et al.*, 1988), except that the typically Villafranchian taxa began to disappear at this time (Gliozzi *et al.,* 1997). Significantly, this unit marks the arrival and widespread dispersal of two new *Canis* species into Western Europe: *Canis arnensis* Del Campana, 1913, and *Canis falconeri* Forsyth-Major, 1877 (Azzaroli, 1983; Azzaroli *et al*., 1988; Gliozzi *et al.,* 1997). The site of Senèze in France, which contains the aforementioned *Canis senezensis*, is considered to lie between the Olivola and Tasso F.U.s. This canid is represented by two maxillary bones with complete dentition (Rook and Torre, 1996a), and was diagnosed by its less derived dentition (Sardella and Palombo, 2007). The Late Villafranchian site of Slivnitsa, Bulgaria, has also yielded a canid similar to *C. senezensis* (Sotnikova *et al.,* 2002).

It has been suggested that *C. senezensis* is a less derived form of *Canis arnensis* (Sardella and Palombo, 2007), with the former lying within the size range of the latter (Rook and Torre, 1996a). The Khapry wolf *C*. cf. *senezensis* was also found to be within the upper size range of *C. arnensis* (Sotnikova *et al*., 2002). However, Garrido and Arribas (2008) believed the remains of *C. senezensis* showed no anatomical or metric differences to *C. arnensis* and thus considered it synonymous. However, there are numerous issues with the age of the faunas present at Senèze (and thus the age of *C. senezensis*), since the assemblage contains

a mix of both Middle Villafranchian and Late Villafranchian elements (see also Azzaroli *et al*., 1988; Rook and Torre, 1996a).

The site of Fonelas P-1 site in Granada, Spain, correlated to c. 1.9-1.7 Ma (Garrido and Arribas, 2008) and of similar age to the Italian Upper Valdarno, has produced three sympatric canids: *C. etruscus* and *C. falconeri* (both present in the Tasso F.U.) and a new species, *Canis accitanus* Garrido and Arribas, 2008. This is the smallest member of the genus *Canis*, sharing some basic morphological features with *C. arnensis* from the Tasso F.U. but equally possessing unique anatomical features (Garrido and Arribas, 2008). The presence of *C. etruscus, C. arnensis, C. falconeri*, as well as the putative *C. senezensis* and the small *C. accitanus* of Spain, therefore reveal a large and diverse European canid guild at this time.

The subsequent Faunal Units in Italy of the Late Villafranchian include the Farneta and Pirro Nord F.U.s (Gliozzi *et al*., 1997). The site of Pirro Nord is especially important, since it has one of the earliest co-occurrences of *Canis mosbachensis* Soergel, 1925 and *Canis* (*Xenocyon*) *lycaonoides* Kretzoi, 1938 (Petrucci *et al*., 2013). The *C. mosbachensis* remains from Pirro Nord share similar features with the late Early Pleistocene (Epivillafranchian) site of Untermassfeld in Germany, whereas *C.* (*X*). *lycaonoides* was found to be slightly smaller in post-cranial dimensions than its counterparts at Untermassfeld (Petrucci *et al*., 2013) (see later). The Pirro Nord F.U. has been dated to between 1.7-1.3 Ma (Arzarello *et al*., 2009), although 1.5-1.3 Ma has equally been suggested (Bertini *et al*., 2010). .

Another early appearance of *C. mosbachensis* was at Venta Micena, Spain (Rook and Martinez-Navarro, 2010), dated to between the Jaramillo and Olduvai subchrons (1.77-1.22 Ma) through palaeomagnetism and supporting biochronology, and to 1.37 ±0.24 Ma on combined U-series and electron spin resonance methods on teeth (Duval *et al*., 2011).

2.1.3.4. The Epivillafranchian and the Galerian

The transition between the Villafranchian and the succeeding Land Mammal Age, the Galerian, has been termed the Epivillafranchian, correlated to 1.2-0.9 Ma (late Early Pleistocene) and with the distinctive character of the fauna supporting the designation of a separate chronostratigraphical unit (Kahlke, 2000; Kahlke *et al*., 2011). Typical sites of the Epivillafranchian include Apollonia-1, Greece and Untermassfeld. The small *Canis apolloniensis* Koufos and Kostopoulos, 1997 has been identified from Apollonia-1, along

with *Canis* (*Xenocyon*) *lycaonoides*. However, Garrido and Arribas (2008) considered that *C. apolloniensis* may represent an early record of the small Middle Pleistocene *Canis mosbachensis* Soergel, 1928, which is also found at Untermassfeld.

The Galerian (early Middle Pleistocene, originally covering 1.2-0.6 Ma) is characterised by a distinct and uniform fauna, including many extant taxa (Azzaroli *et al.,* 1988; Gliozzi *et al.,* 1997). It has been compared to the British Cromerian, also of early Middle Pleistocene age (Azzaroli *et al.*, 1988). In Italy, faunal units representing the Galerian include the Colle Curti, Slivia, Isernia and Fontana Ranuccio F.U.s. (Gliozzi *et al*., 1997). Although *C. mosbachensis* and *C.* (*X.*) *lycaonoides*, together with the addition of *Cuon priscus* Thenius, 1954, were considered to typify Galerian assemblages (Azzaroli *et al.*, 1988), the first two species are now recognised from as far back as the Late Villafranchian. These taxa were formerly considered to have their progenitors in the Late Villafranchian faunas of Eurasia, with *C. mosbachensis* a descendent of *C. etruscus* (Azzaroli *et al*., 1988), and *C*. (*X*)*. lycaonoides* a descendent of *C. falconeri* (Masini and Torre, 1996).

2.1.3.5. The Aurelian

The most recent Land Mammal Age is the Aurelian, representing the Late Middle Pleistocene onwards. In Italy, the faunal units of Torre in Pietra and Vitinia (Gliozzi *et al*., 1997; Palombo *et al*., 2003-2004) characterise this period. The site of La Polledrara di Cecanibbio (Gliozzi *et al*., 1997) correlated with Marine Oxygen Isotope Stage (MIS) 9 and of coeval age to the site of Torre in Pietra (Anzidei *et al*., 2011) (and thus the Torre in Pietra F.U.) marks the first appearance in Italy of *Canis lupus*. No remains of *C. lupus* have been identified from MIS 9 in Britain, with only the smaller *C. mosbachensis* present in sites such as Grays Thurrock and Cudmore Grove (Schreve, 2001a). The oldest British record of *C. lupus* is from Pontnewydd Cave in north Wales (Currant, 1984; Turner, 1995a), which has been correlated to MIS 7 based on a thermoluminescence dating estimate of 225 +89/-47 Ka within the Lower Breccia (Schwarcz, 1984). Its appearance marks a dramatic increase in body size when compared to the smaller remains of *C. mosbachensis* from the early Middle Pleistocene (Turner, 1995a).

2.2. The origin and evolution of hunting-related adaptations

The origins and evolution of sociality and cursoriality in canids will be introduced in the following section, including the characteristic cranio-dental adaptations for hunting seen in the Canidae.

2.2.1. The origin and evolution of sociality

As previously stated, modern wolves exhibit sociality, which is a common behaviour amongst the larger members of the extant Canidae (including *C. alpinus* and *L. pictus*). Sociality may have its roots in the increase in encephalisation seen in the Caninae at the Miocene-Pliocene boundary (c. 5.33 Ma), which also coincides with the diversification of the Caninae and subsequent Eurasian expansion (Finarelli 2008). The main selective pressures behind group living in carnivores are the need for cooperative hunting (to combat constraints of prey availability and abundance), defence of territory and prey, and defence against other predators (Macdonald, 1983). In general, cooperative hunting by wolves enables the apprehension of prey larger than themselves (Macdonald, 1983; Van Valkenburgh and Koepfli, 1993; Andersson, 2005). In contrast, Schmidt and Mech (1997) proposed that modern wolves do not live in packs to facilitate predation on large animals, but because adult pairs can efficiently share excess food with their maturing offspring, termed as the 'kin selection' hypothesis. This hypothesis was based on how single wolves have the ability to kill large prey alone, and how pairs of wolves acquire more food per wolf on average than those in a larger pack (Schmidt and Mech, 1997).

Similarly, Sand et al. (2006) considered that hunting group size (where the addition of more members improved success, as proposed by Janis and Wilhelm, 1993), was not an important factor, since numerous other variables (e.g. type of prey, age and sex of prey, prey group size, as well as environmental factors such as season, habitat type and weather) might be more influential for kill success rates (Sand *et al.,* 2006).

2.2.2. The origin and evolution of cursoriality

Modern wolves are pursuit predators, which Ewer (1973) defined as those that chase their prey for a distance of greater than 300m. In general, chases range from 100m to 5 - 6km (Mech, 1974; Mech and Korb, 1978), thus emphasising wolves' adaptations for swift running on relatively open terrain (Ewer, 1973). Wolves are cursorially-adapted, a general

term that includes a specific set of morphological features such as relatively long distal limb segments combined with reduced ulna and fibula, compressed or absent lateral metapodials and phalanges, a reduced range of limb motion relative to the sagittal plane, and finally, in carnivores, a change in foot position from the primitive plantigrade to the digitigrade (Garland and Janis, 1993). Longer metapodials are also considered a cursorial adaptation (Hildebrand, 1952), as well as shorter, rather than longer, phalanges in order to facilitate sustained speed (Van Valkenburgh, 1987).

The origins of cursoriality in canids was not congruent with, but followed the global spread of modern grassland-dominated ecosystems by the Miocene-Pliocene boundary (c. 5.33 Ma) and the accompanying diversification of cursorial ungulates (Andersson, 2005). The movement and migration of prey was likely a contributing factor, and in order to pursue prey over large distances either daily or seasonally, predators ultimately developed both cursorial morphology and the capacity for sustained running (Janis and Wilhelm, 1993). However, Janis and Wilhelm (1993) have emphasised that modern pursuit predator behaviour was not a consequence of long term selection for progressively more cursorial locomotion, nor related to co-evolution between ungulates and carnivores, but is a rather more recent development, related to climate change over the last few million years. In particular, the Late Pliocene experienced significant global cooling, echoed by the development of modern types of desert and semi-desert, as well as extensive temperate grasslands. The colder and more arid conditions of the Plio-Pleistocene caused the emergence of migratory behaviour in ungulates such as reindeer, wildebeest and zebra, with predators forced to follow suit (Janis and Wilhelm, 1993).

2.2.2.1. Identifying cursoriality in the fossil record

The metatarsal to femur ratio (MT/F) has been used as an index of cursoriality in mammals (Van Valkenburgh, 1987; Garland and Janis, 1993; Janis and Wilhelm, 1993), where the ratio reflects the degree to which the distal elements of the hind limb are elongated relative to the proximal elements (Garland and Janis, 1993). Larger MT/F values were considered to indicate increased cursoriality (Garland and Janis, 1993), and generally cursorial mammals were found to have larger MT/F ratios than non cursorial ones, although this was complicated by phylogenetic relationships (Garland and Janis, 1993).

However, little empirical evidence exists indicating the relationship between the MT/F ratio and locomotor performance (Garland and Janis, 1993), and within cursorial mammals, it is

unclear whether limb proportions or lengths are even significant predictors of locomotor performance overall (Garland and Janis, 1993). Andersson and Werdelin (2003) and Andersson (2004a; 2005) instead used the functionally-important humeral trochlea to indicate cursoriality. In modern canids, the morphology of the trochlea only allows limited rotation of the radius, thereby reducing the ability of canids to supinate their forelimb (and grapple with prey) but enhancing running capacity. Andersson (2005) found that Tertiary canids retained the ability to supinate their forearms, indicating that their hunting behaviour included the manual manipulation of prey, similar to modern pantherine cats rather than modern canids, and indicating that they were not pursuit predators at this time (see also Garland and Janis, 1993). The subsequent loss of supination in members of the Caninae resulted in the inability to use forelimbs for grappling or manipulating prey, which suggests a trade-off between cursoriality and prey apprehension (Andersson and Werdelin, 2003).

2.2.3. Classification of carnivory

All members of the Canidae are considered carnivorous, i.e. their diet includes a substantial proportion of flesh and they possess carnassial dentition (Savage, 1977). However, the proportion of flesh in the diet compared to other non-flesh foods such as invertebrates, fruit and vegetable materials can vary. To quantify these varying proportions, Van Valkenburgh (1988a, 1989) devised broad dietary categories classifying the level of carnivory according to the percentage of flesh (i.e. meat) to other foodstuffs (Table 2.1).

Dietary category	**Description**
1. Meat	>70% meat
2. Meat/bone	>70% meat with the addition of large bones
3. Meat/non-vertebrates	50-70% meat with fruit and/or insects
4. Non-vertebrates/meat	<50% meat with fruit and/or insects predominating

Table 2.1. Dietary categories defining carnivores as devised by Van Valkenburgh (1988a, 1989).

Turner (1995b) similarly developed dietary categories for large carnivores, namely 1). flesh eaters (predominantly flesh consumed), 2). carcass destroyers (able to eat bone and destroy carcasses) and 3). bone eaters (able to eat bone), however, Van Valkenburgh's more detailed scheme will be applied here.

Modern *C. lupus* belongs to the first dietary category, which also includes hunting dog *Lycaon pictus,* Asiatic dhole *Cuon alpinus* and bush dog *Speothos venaticus*. These canids are identified as being hypercarnivorous, whereby their diets consist almost exclusively of

vertebrate flesh and they possess moderately- to greatly-reduced cheek teeth with a slicing function (Van Valkenburgh, 1991).

In particular, *L. pictus, C. alpinus* and *S. venaticus* all exhibit a further modification of the m1 carnassial, known as a trenchant heel (Ewer, 1973; Van Valkenburgh, 1991). In the extreme version of the condition, the talonid basin of the m1 has a single large, centrally-positioned, blade-like cusp (hypoconid) (Van Valkenburgh and Koepfli, 1993). Associated with the development of the m1 trenchant heel in canids is the reduction of the post-carnassial grinding area, involving diminution of the m1 metaconid and the M1 hypocone, as well as the presence of moderate to small premolars (Van Valkenburgh, 1991). The functional significance of the trenchant heel is the lengthening of the effective cutting blade of the carnassials (Van Valkenburgh, 1991). Combined with the reduction of the grinding areas in the post-carnassial molars, the mechanical advantage of the chewing muscles at the carnassials is improved (Ewer, 1973), and hence meat slicing is faster and more efficient. The modification of the m1 talonid therefore indicates a highly predatory habit with a decreased importance of vegetable foods in the diet (Ewer, 1973).

However unlike the other hypercarnivorous canids, *C. lupus* has retained a bicuspid m1 talonid, maintaining the dual slicing and crushing purpose of the lower carnassial and thus enabling a more generalist diet. The following section will introduce the cranio-dental characteristics of *C. lupus*.

The evolution of blade-like carnassials has occurred many times from the Eocene to the Pleistocene, with driving factors including reduced competition due to the absence of felids, as well as increased intraspecific competition (Van Valkenburgh, 1991). It is significant that canids never developed the wholly specialised dentition found in felids, and that they retained the post carnassial molars and m1 talonid. By retaining these features, canids are afforded comparatively greater dietary flexibility and coping mechanisms when faced with changes in prey availability, and ultimately, have more versatility and evolutionary freedom (Van Valkenburgh, 1991).

2.2.4. Cranio-dental adaptations for hunting and diet

The extreme variability and diversity within the Carnivora is reflected in the size and shape of the cranium and dentition (Meiri *et al.,* 2005). Canid dentition is less reduced and less specialised than in most other carnivore families (Hillson, 2005) and is adapted for the

killing of prey and fast slicing of meat, as well as crushing hard-to-chew material such as bone and tendon, as well as some vegetable foods (Ewer, 1973; Stahler *et al.,* 2006).

In general, canids share the dental formula I3/3, P4/4, M2/3 and are broadly similar in terms of overall morphology (shown in Figure 2.2). In all canids, the upper and lower teeth are not in direct alignment above one other, but interdigitate, with the lower slightly in advance of the corresponding upper (Ewer, 1973). By using the dental apparatus of modern *C. lupus* as an analogue for function in the Pleistocene canids, comparisons can be made regarding the potential variability in diet.

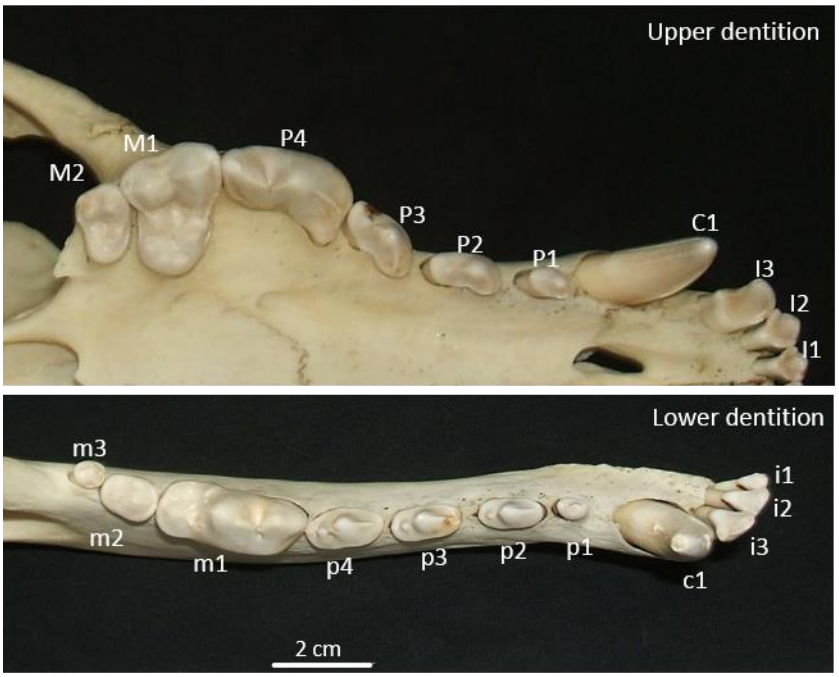


Figure 2.2. Upper and lower dentition of *C. lupus*, illustrating the numbering and positioning of each tooth.

The cranio-dental morphology of modern *C. lupus* reflects its hypercarnivorous diet, as well as its adaptability. The pointed canines and incisors have the dual function of holding prey and tearing flesh whilst the sectorial premolars act both to pierce and hold prey (Ewer, 1973). The function of the premolar complex is quantified by p1-p4 and p2-p4 lengths in the mandible and P1-P4 length in the maxilla, and thus an increase in the length of these complexes may relate to piercing and holding prey. Changes in the cheek tooth row overall p1-m3 and p2-m3 lengths may also be reflected. In some carnivores, changes in the shape of the largest lower premolar (p4) have been related to bone-eating behaviour based on the premise that flesh specialists such as felids tend to have smaller, narrower premolars in comparison to bone specialists such as hyaenas, which have enlarged, more rounded and robust premolars (Van Valkenburgh, 1988a, 1989, 1991; Werdelin, 1989).

Hyaenas have specifically adapted premolars for bone-cracking, defined by Werdelin (1989) as the breaking open of bones by the point-to-point contact between cheek-tooth cusps in order to obtain the marrow inside. In contrast, modern canids are adapted for bone-crushing, defined by Werdelin (1989) as the area-to-area grinding of bones between flattened teeth, generally the post-carnassial molars. Both modern hyaenas and canids utilise bone for marrow extraction, yet access is dictated in different ways by their dental morphology.

Nonetheless, on occasion, hyaenas have been known to use their incisors or carnassials (m1, P4) to break ribs and scapulae, which are less massive in comparison to limb bones (Van Valkenburgh, 1996). Thus, despite bone cracking adaptations, certain bones are processed using the wider dental complex. Wild dogs were also found to use both their carnassials and the crushing apparatus of the post-carnassial molars to crush bone (Van Valkenburgh, 1996). It therefore appears that in order to access marrow, more than one dental region can be used to acquire this resource, depending on the type of bone exploited. Thus, as in other canids, teeth such as the p4 (which has an overlapping position below the anterior upper carnassial and is situated in the anterior region of maximum bite force), may become involved in bone use, together with the molar crushing apparatus. However, the regular involvement of teeth other than molars in this process is likely to stem from dietary stress, whereby increased access to marrow is necessary.

The morphometric ratio of premolar shape (PMD: p4 width/p4 length) was used by Van Valkenburgh (1988a, 1989, 1991) to infer the relative proportion of bone in the diet, with rounder premolars indicating a diet incorporating more bone, as opposed to narrower premolars indicating a flesh-only diet.

However, notwithstanding controversies relating to the use of ratios in taxonomical and ecological analysis (see section 4.5.5), the same premise would also suggest that any increase in bone-eating should be reflected by changes in the length and width of p4, analysed as linear measurements rather than ratios. Changes in length and width may also be followed by changes in jaw strength, especially at the p3-p4 junction, as well as a potential increase in the size of the molar apparatus and the carnassials. Changes in p4, however, may also relate to changes in the carnassials. The partial occlusion of the posterior p4 with the anterior P4 may indicate a close relationship with carnassial function, for example, an increase in m1 trigonid and P4 blade may require an increase in p4 length.

The carnassial teeth are specifically adapted to work together for cutting flesh, with the paracone and metacone cusps of P4, and the trigonid cusps of m1 all laterally flattened to enable a shearing action (Ewer, 1973). Hence, the carnassial pair is particularly informative regarding the relative proportions of flesh consumed. Unlike the P4, the m1 is of dual functionality based on its position with respect to the upper jaw, with both P4 and anterior M1 occluding (Ewer, 1973). The end result is incorporation of both slicing capacity (the m1 anterior trigonid 'blade' with the P4) and crushing actions (the posterior talonid basin 'heel' with the anterior M1).

Changes in length of the m1 trigonid or the P4 length may therefore specifically relate to the amount of flesh incorporated in the diet, since typically, flesh and bone specialists tend to have longer cutting blades in comparison with more omnivorous species (Van Valkenburgh, 1988a; Van Valkenburgh and Koepfli, 1993). Lengthening of the trigonid also gives increased ability to slice flesh quickly (Van Valkenburgh, 1991), which may confer a competitive advantage. Changes in carnassial width may relate to either strengthening (in order to reinforce this integral tooth pair), or to an increase in slicing ability. In association with the P4, the P3 may also have some functionality with the carnassial group, as well as occluding with the p3-p4 region.

The molars, especially the upper molars, have a crushing function (Ewer, 1973), which also involves the m1 talonid and m2. This function relates to the consumption of non-flesh foods, and hence reflects the relative proportions of such in the diet. For example, hypercarnivorous species such as felids tend to have reduced post-carnassial molars, whereas the opposite is true for more omnivorous species (Van Valkenburgh, 1991). The size of molars present can therefore indicate the type and variability of diet. Figure 2.3 illustrates the cusp morphology of a). P4, M1 and M2, and b). p4, m1 and m2.

The combination of shearing carnassials and canines in the canid dentition requires complex jaw action and musculature, with the canines and surrounding anterior teeth requiring an open jaw and a hinge-like closure with sufficient force to enable a powerful bite with the canines, whilst the carnassial pair require the jaw to be closed, with a lateral jaw movement for shearing (Ewer, 1973). Bite force is related to the specialisation of hunting larger prey (Christiansen and Wroe, 2007) and hypercarnivores like *C. lupus* tend to have relatively deep jaws, to cope with increased loading from killing and feeding on large prey (Van Valkenburgh *et al*., 2004). The presence of large dentary depths between p3-p4 and m1-m2 can therefore allow the size of prey taken to be inferred. The p4 may also

reflect changes in bone utilisation, since it is located in the anterior region of maximum bite force in the mandible (Werdelin, 1989).

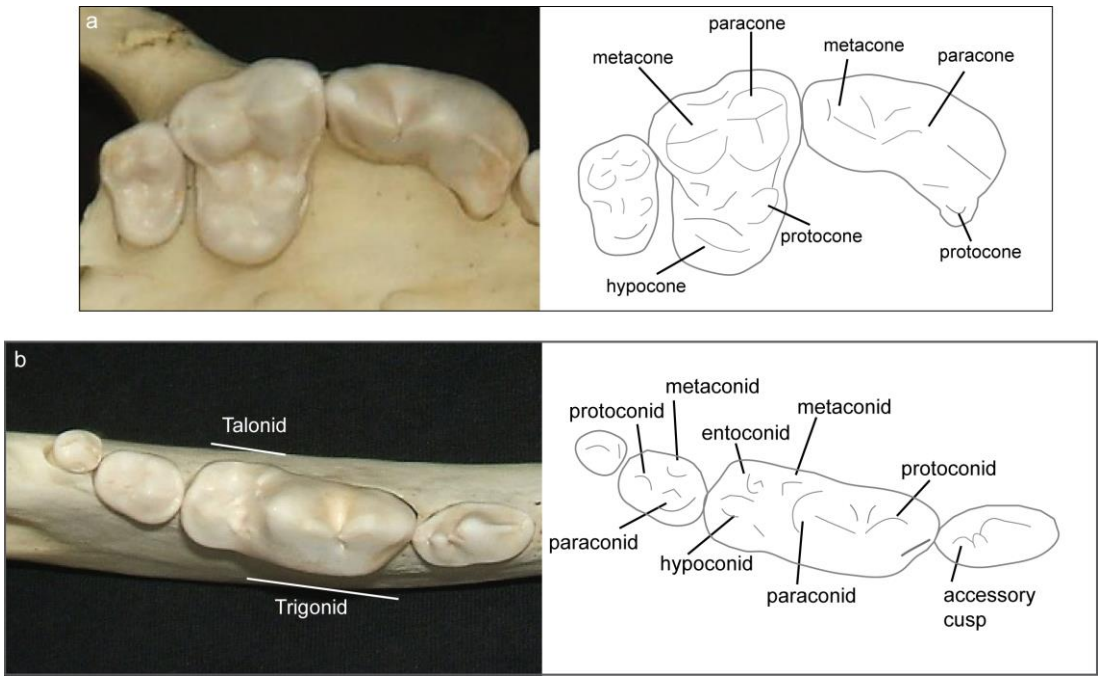


Figure 2.3. Cusp morphology of the upper and lower carnassials and molars a). P4 and M1, b). p4, m1 and m2.

2.3. Taxonomy and morphological comparisons of the four main analysed canids

Systematic Palaeontology

Class: MAMMALIA Linnaeus, 1758

Order: CARNIVORA Bowdich, 1821

Family: CANIDAE Fischer von Waldheim, 1817

Subfamily: CANINAE Fischer von Waldheim, 1817

Genus: *Canis* Linnaeus, 1758

2.3.1. *Canis etruscus* Forsyth-Major 1877

2.3.1.1. Composite morphological descriptions from Olivola and the Upper Valdarno

Feature	Description
Cranium	Elongated snout, narrow between the orbits, broad frontals. Orbits moderate size, well-developed sagittal and nuchal crest, neurocranium generally rounded, occipital region moderately sized.

Upper dentition	C1 curved, mesial ridge often well developed, with tubercle. P2 and P3 paracone anterior crest in oblique lingual position, with posterior ridge connecting to posterior accessory cusp and developed posterior cingulum. P4 anteriorly positioned small rounded protocone, aligned with anterior paracone, crest running from protocone connecting to anterior crest on front of paracone, paracone slightly rounded, metacone elongated, angled diagonally in buccal direction, metastyle of metacone often in contact with edge of M1, well-developed lingual cingulum ridge. M1 squared shape with well-developed buccal cingulid; paracone well developed; wide basin area with well-developed protocone; furrow separating it from metaconule, metaconule moderately developed, paraconule less so, hypocone large, wedge-shaped. M2 moderately developed buccal cingulid, paracone and protocone well developed.
Mandible	Moderately thick mandible, narrower and less robust than modern *C. lupus*. Incisor row is slightly curved, premolars aligned straight in the mandible, with p4 overlapping anterior m1. From m1, the molar row is curved lingually in comparison to premolar row. Premolar teeth are generally quite closely spaced.
Lower dentition:	c1 relatively short, slight posterior curve, small tubercle and a defined mesial ridge. p1 anterior crest on paraconid, with slight posterior ridge connecting to small posterior cingulum. p2 slight basal anterior cusp above cingulum margin, anterior crest front of paracone, posterior ridge to slight posterior cingulum. p3 similar, posterior ridge connects to moderately developed accessory posterior cusp, with small posterior cingulum margin, lingual cingulum present, p3 similar lateral level to p2 and p4. p4 broader, small cusplet basally above cingulum margin, anterior crest present on front paraconid, well developed accessory cusp, with variable small second accessory cusp in front of posterior cingulum, lingual cingulum present. m1 paraconid positioned lower than protoconid; protoconid more conical shape, posterior protocristid to metaconid; metaconid prominent; ridge present opposite metaconid buccally terminating in a small 'bump', talonid basin moderately wide, well-developed hypoconid with antero-posterior crest, at base trigonid crests form an asymmetrical 'V' shape, one leg partly forms the 'bump' and ridge opposite metaconid, other forms oblique cristid towards the metaconid. Hypoconid and entoconid linked by sinuous transverse cristid, lingual crest connects entoconid to base trigonid, occasionally bumpy, slight low posterior ridge present at most posterior edge of talonid where m2 meets. m2 rectangular to sub-rectangular shape; anterior cingulid around paraconid; plus well-developed antero-buccal cingulum below paraconid; subequal cusps, paraconid and protoconid well developed.

Table 2.2. Composite morphological description of cranio-dental features of *C. etruscus* from Olivola (Olivola F.U.) and the Upper Valdarno sites (Tasso F.U.) based on personal observations of the material. Sample size: 21 individuals (see Table 5.2).

2.3.1.2. Comparisons with other Pleistocene canids based on personal observation and literature review

Due to lack of material and deformation of cranial specimens, full comparison of cranial features in *C. etruscus* was difficult. Nonetheless, the forehead of *C. etruscus* was laterally more inclined than that of *C. arnensis*, echoing the receding forehead found in the Pantalla specimens recorded by Cherin et al. (2013a). In comparison to modern *C. lupus*, *C. etruscus* had broader and thicker frontals with the posterior edges of the frontals more defined, which Sotnikova (2001) considered to be a less derived feature of *Canis*. Overall, the general cranial dimensions of *C. etruscus* were similar to those of *C. mosbachensis*. Although it could not be seen in the material used here, Cherin et al. (2013a) reported that the zygomatic arches were more slender and curved in the Pantalla *C. etruscus* than in *C. mosbachensis*.

The P4 anterior protocone was moderately large and situated more anteriorly, level with the paracone base and in a similar position to *C. mosbachensis* (Sotnikova, 2001). In comparison to *C. arnensis*, the metacone was more elongated and slightly narrower. The metastyle was moderately developed and broad in *C. etruscus*, and was often in contact with the M1, as found in the Pantalla specimens by Cherin et al. (2013a). The M1 in *C. etruscus* was well developed and squarer than in *C. arnensis*, with a prominent and enlarged paracone relative to the metacone. This was described as a significant feature of *C. etruscus* by Tedford et al. (2009) and was considered typical of the *etruscus-mosbachensis* group by Cherin et al. (2013a). Both the buccal cusp area and lingual basin area are larger and deeper than in *C. mosbachensis* and *C. lupus* (Cherin *et al*., 2013a). Cherin et al. (2013) also considered the shape of M2 to be diagnostic, being squarer in *C. etruscus*, and more 'bean' shaped in *C. arnensis*.

The lower mandible was narrower and less robust than in modern *C. lupus*. The p3 in some specimens of *C. etruscus* was found to be positioned slightly lower in the mandible than the p2 and p4, a characteristic also seen in *C. mosbachensis* from Untermassfeld (Sotnikova, 2001) (see also Tedford *et al*., 2009). However, this feature was not found in the Olivola specimens (as also noted by Sotnikova, 2001) but was detected, more surprisingly, in some *C. arnensis* specimens in the present study.

The p4 of *C. etruscus* often possessed a small secondary accessory cusp positioned in front of the posterior cingulum. This less derived feature was also present in *C. mosbachensis* (Sotnikova, 2001; Tedford *et al*., 2009) but is absent in modern *C. lupus*, where this small

secondary accessory cusp cannot be differentiated from the posterior cingulum (Tedford *et al.,* 2009). However, not all *C. etruscus* specimens had this feature and instead, the posterior cingulum was more pointed in shape, with the secondary cusp indistinguishable, similar to modern *C. lupus*.

The m1 paraconid was shorter and narrower in comparison to the protoconid, whilst the metaconid was more prominent lingually than in modern *C. lupus,* with its larger size similar to *C. mosbachensis* (Sotnikova, 2001). The talonid basin was more complex in *C. etruscus* than in *C. lupus*, and shares more similarities with *C. mosbachensis*. The well-developed hypoconid has a slight antero-posterior crest, defining the edge of the hypoconid. This culminates anteriorly on the hypoconid as an asymmetrical 'V' or 'U' shape, whereby the buccal leg of this ridge forms the ridge and 'bump' on the buccal side of the posterior trigonid, which is a shared feature with *C. mosbachensis* (Martinez-Navarro *et al.,* 2009). The more lingual leg of this hypoconid ridge forms the oblique cristid, which runs towards the metaconid across the talonid basin. This is also a less derived trait often present in *C. mosbachensis*. A sinuous cristid links the hypoconid to the smaller entoconid, also a shared feature with *C. mosbachensis* (Martinez-Navarro *et al.,* 2009). Also, a lingual cristid is also present between the lingual entoconid and the metaconid, which in some specimens appears 'bumpy'. This feature is again similar to *C. mosbachensis,* although with the latter often having two small tubercles between the metaconid and entoconid (Martinez-Navarro *et al.,* 2009).

The m2 of *C. etruscus* has an antero-buccal cingulum, often found in *C. mosbachensis*, but missing in modern *C. lupus* (Sotnikova, 2001). Both *C. etruscus* and *C. arnensis* also possess an anterior cingular external border on the m2, appearing as a buccal 'shelf' on the side of the tooth below the paracone. This feature is more developed in *C. etruscus* and *C. mosbachensis* but is only weakly present in *C. arnensis* (see also Martinez-Navarro *et al*., 2009).

2.3.2. *Canis arnensis* del Campana 1913

2.3.2.1. Composite morphological description from the Upper Valdarno

Feature	Description
Cranium	Sloping forehead into relatively narrow snout. Moderately broad frontals. Sagittal and nuchal crest well developed. Small rounded neurocranium. Small orbits. Upper premolars well- spaced in maxilla, incisors curved inward lingually.

Upper dentition	I3 has small mesial ridge with lingual ridge along cingulum margin. C1 relatively straight with slight mesial ridge. P1 oblique anterior lingual ridge. P2 oblique anterior lingual ridge up front paracone, posterior ridge to cingulum. P3 similar, with posterior accessory cusp and posterior cingulum. P4 protocone well developed, often positioned separately from paracone anteriorly, anterior crest front of paracone, paracone angled in slight posterior direction, narrow conical shape, metacone is longer and curved buccally, well-developed lingual cingulum. M1 has a moderately developed buccal cingulid, paracone well developed, well-developed hypocone, moderate protocone with crest to metaconulid, deep furrows between cusps. M2 has a moderate buccal cingulid, buccal cusps of similar size, moderate protocone and hypocone in basin, slight ridge from protocone connecting to buccal cingulid.
Mandible	Narrow mandible, narrow below the molars. Premolars aligned straight in mandible and well-spaced. p4 overlaps anterior m1. Molar row slightly curves at m1, although in alignment with premolars.
Lower Dentition	c1 curved in posterior direction, slightly thickened at cingulum margin, slight mesial ridge with less developed tubercle. p1 round, slight posterior cingulum bulge. p2 anterior ridge up front paraconid, posterior ridge and small cingulum bulge. p3 similar, plus small anterior lingual basal protonid, posterior ridge to small accessory cusp, with a slight post cingulum ridge and lingual cingulum. p4 similar p3, but broader shaped, well developed posterior accessory cusp, plus often a small to moderately secondary accessory cusp in front of posterior cingulum. m1 paraconid similar level to tip p4 protoconid, m1 protoconid conical shape, with anterior crest up front, slight posterior protocristid to metaconid, metaconid well developed, talonid with well-developed hypoconid, antero-posterior ridge often at base of trigonid forming slight 'V' shape, one leg forming slight ridge opposite metaconid, other the oblique cristid towards metaconid, transverse cristid often absent between hypoconid to entoconid, crest between entoconid to metaconid, m2 sub-rectangular, slightly curved; subequal cusps; anterior cingulid around paraconid and metaconid, very slight antero buccal cingulum, paraconid and protoconid well developed. m3 round shape.

Table 2.3. Composite morphological description of cranio-dental features of *C. arnensis* from the Upper Valdarno sites (Tasso F.U.) based on personal observations of the material. Sample size: 8 individuals (see Table 5.2).

2.3.2.2. Comparisons with other Pleistocene canids based on personal observation and literature review

Like *C. etruscus*, *C. arnensis* also had moderately broad frontals, although with a lower, less-inclined forehead. *C. arnensis* possessed a longer, narrower snout and palate than *C.*

etruscus and the upper premolar row had wider diastemata than in *C. etruscus* and *C. mosbachensis*. The P4 protocone was more separated from the paracone lingually than in *C. etruscus*, and in some specimens it was also level with the anterior of the paracone. The M1 was characterised by a large basin, more lingually elongated than the squared shape in *C. etruscus*. The buccal cingulid was also less well developed in *C. arnensis* and the hypocone appeared as a more defined cusp instead of the large wedge-like shape seen in *C. etruscus*.

C. arnensis had a narrower, thinner jaw than some specimens of *C. etruscus*. Interestingly, both *C. arnensis* and the Upper Valdarno *C. etruscus* shared the small secondary accessory cusp present on the posterior p4, although its presence is variable in both Upper Valdarno canids, as mentioned earlier regarding Olivola. The m1 in *C. arnensis* was generally narrower than in *C. etruscus*. The protoconid tip was approximately level with the p4 paraconid, with a straighter edge effectively levelling off the cusp edge. This was also seen in *C. etruscus*, although the protoconid tip was often slightly more elevated. Both are in contrast to *C. lupus*, where the p4 protoconid is generally higher than the paraconid and more pointed, with an inclined cusp edge.

In general, the talonid morphology was less complex than in *C. etruscus* and *C. mosbachensis*, with some features more variable. In some specimens the hypoconid and entoconid of the m1 talonid were connected by a slight crest. Martinez-Navarro *et al*. (2009) described these cusps as isolated in *C. arnensis* but its occurrence in specimens examined here suggests that this was a variable feature of the species. Like *C. etruscus*, a buccal ridge originating from the talonid and situated on the posterior surface of the trigonid, opposite the metaconid, was also present in two specimens of *C. arnensis* examined. However, according to Martinez-Navarro *et al*. (2009), this feature should be absent in *C. arnensis* and this may again be an example of intraspecific variation. As with *C. etruscus,* a crest was also present between the entoconid and the metaconid on the talonid*,* although missing the associated tubercles found in *C. mosbachensis* (Martinez-Navarro *et al*., 2009).

2.3.3. *Canis mosbachensis* Soergel, 1925

2.3.3.1. Composite morphological description from Untermassfeld and the Cromerian Complex sites

Feature	Description
Cranium	Moderately long narrow snout, narrow between the orbits. Frontals moderately thick and wide, sagittal crest moderately well-developed, with well-developed nuchal crest. Rounded neurocranium, moderately wide palate.
Upper dentition	C1 slight to well-developed mesial ridge and tubercle, slight posterior curve, moderately spaced premolars. P1 anterior ridge in oblique lingual position, posterior ridge and lingual cingulum. P2 anterior ridge in oblique lingual position, posterior ridge to cingulum, also present lingually. P3 similar, posterior crest to small accessory cusp, rounded posterior cingulum, with moderate lingual cingulum connected. P4 rounded protocone, on level anterior paracone, slight crest onto paracone, connecting to main crest up front paracone, narrow paracone, moderately short metacone, moderately developed lingual cingulum along metacone. M1 moderately to well-developed buccal cingulum, paracone well-developed, moderately wide basin, moderately developed protocone, well developed ridge to small metaconulid, and ridge to small paraconulid; moderate hypocone, slight ridge shape, deep furrow between hypocone and protocone. M2 more curved bean shape, moderately developed buccal cingulum, in basin moderately developed hypocone and protocone, rounder, flatter shape.
Mandible	Moderately narrow jaw, premolar teeth aligned to each other straight in jaw, whilst row overall lightly buccally curved and slightly spaced. p4 overlaps anterior buccal m1. Molar row curves in lingually.
Lower dentition	c1 curved slightly posteriorly, slight mesial ridge with tubercle, slight posterior crest inside curve. p1 low height, anterior to posterior ridge, lingual cingulum bulging. p2 anterior ridge to posterior ridge to flared out posterior, slight cingulum. p3 similar, more narrow tapered paraconid, more sloping posteriorly, posterior ridge to small accessory cusp. p4 set higher level, anterior ridge, paraconid sloping slightly posteriorly, well-developed accessory cusp, with smaller secondary accessory cusp defined from posterior cingulum, lingual cingulum developed. m1 paraconid positioned higher than p4 paraconid, often cusp edge level or inclined, protoconid well developed, frontal crest often present, protocristid to metaconid, metaconid rounded, moderately developed, talonid with subequal cusps, well-developed hypoconid, often slight antero-posterior crest forming 'V' or 'U' shape ridge at base of trigonid, entoconid less developed, variable transverse cristid connecting entoconid and hypoconid, crest from entoconid to metaconid often bumpy, posterior hypoconid shelf present. m2 subrectangular shape, subequal cusps, variable anterior buccal cingulum below paraconid, moderately developed protoconid, crest connecting protoconid to paraconid. m3 round to oval shape.

Table 2.4. Composite morphological description of cranio-dental features of *C. mosbachensis* from Untermassfeld and Cromerian Complex sites based on personal observations of the material. Sample size: 37 individuals (see Table 5.1, 5.2).

2.3.3.2. Comparisons with other Pleistocene canids based on personal observation and literature review

Snout length in *C. mosbachensis* was longer than in *C. arnensis*, although was not possible to compare with *C. etruscus* due to a lack of complete material. The Untermassfeld *C. mosbachensis* had slightly narrower frontals than *C. etruscus* but slightly broader than in *C. arnensis*. Comparisons with British *C. mosbachensis* were not also possible due to lack of complete material.

The P4 protocone was more separate from the base of the anterior paracone than in *C. etruscus*. The M1 was more curved, rounded in shape, and less square than in *C. etruscus*, and more compressed in shape than in both *C. etruscus* and *C. arnensis*. The M1 in *C. mosbachensis* also had a more reduced metaconule than in either of the other species, with a less developed, more ridge-like hypocone (also found by Martinez-Navarro *et al*., 2009). The mandible of *C. mosbachensis* was narrower than in modern *C. lupus*. However, like *C. etruscus*, *C. mosbachensis* from Untermassfeld also had a lower-positioned p3 in the mandible in comparison to the p2 and p4, as did some *C. mosbachensis* specimens from Boxgrove and Westbury-sub-Mendip. Again, as found in *C. etruscus*, the p4 in *C. mosbachensis* often possessed a small secondary accessory cusplet positioned in front of the posterior cingulum, as noted by Sotnikova (2001) and Tedford et al. (2009).

The m1 paraconid tip in *C. mosbachensis* was often higher than the p4 paraconid tip, unlike both *C. etruscus* and *C. arnensis*. The tip was also more variable, either levelled flat (similar to *C. arnensis* and *C. etruscus*) or more pointed (more similar to *C. lupus*). On the buccal side of the posterior trigonid area, a small crest was present from basal area of talonid, also described by Martinez-Navarro et al. (2009). *C. mosbachensis* had a smaller, less developed hypoconid on the m1 talonid than *C. etruscus* and a sinuous crest was present between the hypoconid and entoconid (Martinez-Navarro *et al*., 2009), more common in *C. etruscus* than in *C. arnensis*. The entoconid in C*. mosbachensis* was more reduced in size than in either *C. etruscus* or *C. arnensis* and unlike both other canids, *C. mosbachensis* also had two small tubercles present between the entoconid and metaconid as found by Martinez-Navarro et al. (2009). The m2 in *C. mosbachensis* had a pronounced anterior buccal cingulum below the paraconid, a feature that is more pronounced in *C. etruscus* than in *C. arnensis*, and not present in *C. lupus*.

2.3.4. *Canis lupus* Linnaeus, 1758

2.3.4.1. Composite morphological description from late Middle Pleistocene to present

Feature	Description
Cranium	Oval shaped nasals, moderately elongated snout. Slight to moderate angled stop between snout and forehead. Orbits oval, frontals broad, thick and curved. Well-developed and large sagittal crest, prominent nuchal crest, zygoma kite shaped dorsally, tapered neurocranium, well-developed occipital region, broad palate.
Upper dentition	I3 well developed. C1 slightly posteriorly curved, slight mesial ridge, slight to no tubercle. P1 antero-posterior ridge, slight lingual cingulum. P2 lingual oblique positioned anterior ridge, small posterior accessory cusplet and slight lingual cingulum. P3 similar, with occasional small secondary posterior cusplet as well, separate from posterior cingulum. P4 protocone not separate, bulge on lingual anterior of paracone, well-developed front anterior ridge up paracone, posterior paracone crest into between-cusp valley, metacone comparatively shorter in length, with metacone edge positioned more ling than centre of cusp, slight lingual cingulum. M1 slight buccal cingulum, occasionally small parastyle and metastyle present, paracone well-developed, basin short round shape, slightly compressed, moderately developed protocone, with ridges to small paraconule and small often lacking metaconule, hypocone cusp-like more than ridge, plus smaller cusplets along its lingual position. M2 curved shape, with longer basin, more developed buccal cingulum, soft cusp features.
Mandible	Moderately narrow to thick, coronoid process high and curved posteriorly, ascending ramus moderately thick. Premolar row aligned at slight outward angle in straight line rather than in a curve. p4 overlaps m1 anteriorly, molars angled inward lingually.
Lower dentition	Incisor row on slight curve, i3 well developed. c1 close association with I3, straight rather than recurved shape, very slight mesial ridge, no protruding tubercle. p1 sub-round shape, antero-posterior crest, small posterior cingulum margin. p3 similar, anterior ridge, paraconid sloping posteriorly, often posterior accessory cusp, posterior cingulum, lingual cingulum. p4 set higher than p3, often slight small cusplet at base of anterior ridge up front paraconid, posterior accessory cusp moderately developed, slight posterior cingulum, lingual cingulum. m1 moderately shortened paraconid to protoconid in length, crest up front of protoconid, protocristid to metaconid, metaconid less well-developed, talonid moderately short with subequal cusps, well-developed hypoconid with antero-posterior crest to base trigonid, slight transverse cristid from hypoconid to entoconid, crest between entoconid and metaconid on talonid, often not connecting to entoconid, occasional oblique cristid from hypoconid towards lingual metaconid, slight posterior cingulum edge of talonid. m2 sub-round shape, subequal cusps, well-developed

	central paraconid, slight crest connecting to basinal protoconid. m3 small, rounded shape.

Table 2.5. Composite morphological description of cranio-dental features of *C. lupus* from the late Middle Pleistocene to the present from Britain and mainland Europe based on personal observations of the material. Sample size: 122 individuals (see Tables 5.1, 5.2) of Pleistocene age, and 51 recent individuals from Europe.

2.3.4.2. Comparison with the other Pleistocene canids based on personal observation

The cranium of *C. lupus* is noticeably larger than in *C. etruscus, C. arnensis* and *C. mosbachensis*. The frontals are broad, and bowed ventrally in the centre, more similar to *C. etruscus* rather than *C. arnensis*. Comparisons to *C. mosbachensis* were not possible due to fragmented material. The angle between snout and forehead is more pronounced in *C. lupus*, pulling the forehead more forward than in the other canids. The sagittal and nuchal crests are also high and well developed.

The P4 protocone is small and slight in *C. lupus*, and more joined to the anterior paracone rather than appearing as a separate cusp as in the other canids. The P4 also has a less well developed lingual cingulum. The M1 has a slightly squarer, more lingually compressed basin than in *C. mosbachensis* and *C. arnensis*, although not as square-shaped as in *C. etruscus*. The hypocone is also less wedge-shaped, with a more defined cusp present and smaller bumpy cusplets along its lingual extent. This is in contrast to *C. etruscus* where the hypocone is wedge-shaped, to *C. mosbachensis* where it is a narrow ridge, and to *C. arnensis* where it is a smaller cusp overall. The furrows in the M1 basin are also less defined in *C. lupus*, as well as having a less developed buccal cingulum. In some of the modern specimens, a small M1 parastyle and metastyle are present, which are infrequent in the Pleistocene specimens recorded here.

The mandible in *C. lupus* was more robust than in the other canids, although with some variation between Pleistocene and modern specimens. The p4 often had a smaller basal anterior cusplet present in front of paraconid, not present in the other canids. An extreme case of this was found in Joint Mitnor Cave (Figure 2.4) where the cusp was well developed and similar-sized to the first posterior accessory cusp. The m1 paraconid was more pointed and higher than in *C. etruscus* and *C. arnensis* and the talonid cusps and ridges were more variable in their complexity. Often the complex ridges were similar to those present in *C. etruscus* and *C. mosbachensis*, although simpler talonids, lacking ridge detail, were present in some modern specimens.

Figure 2.4. Right mandibular ramus of *C. lupus* from Joint Mitnor Cave (Torquay Museum P35082), illustrating the presence of an anterior accessory cusp on the p4. Scale: 1cm.

2.3.5. Introducing the Pleistocene canid lineages

C. etruscus, C. mosbachensis and *C. lupus* are believed by many authors to have formed an evolutionary lineage of wolf-like canids (Torre, 1979; Rook and Torre, 1996b; Sotnikova, 2001), based on *C. etruscus* evolving into *C. mosbachensis*, before increasing in size and becoming *C. lupus* during the Middle Pleistocene. The differences between *C. etruscus* and *C. arnensis* are traditionally based on mandibular characteristics, with *C. etruscus* being wolf-like and *C. arnensis* being jackal or coyote-like. *C. arnensis* was originally considered to be jackal-like by Kurten (1968), although this was later revised to coyote-like and more related to *Canis priscolatrans,* an early North American coyote of the late Blancan-Irvingtonian (1.8 Ma) (Kurten, 1974), as well as to the North American fossil coyote *Canis lepophagus* (Kurten 1974). In the current concept of the lineage, *C. mosbachensis* is often considered as the ancestor of modern *C. lupus* (Kurten, 1968; Garrido and Arribas, 2008). However, the phylogenetic position of *C. mosbachensis* is unclear, with closer affiliation to *C. arnensis* proposed (Palombo and Valli, 2003-2004; Garrido and Arribas, 2008), as well as doubt over whether it is a separate species or sub species of *C. lupus* (i.e. *Canis lupus mosbachensis* Thenius 1954, see Kurten, 1968; Lumley *et al*., 1988; Argant, 2009 and later).

Rook and Torre (1996b) considered that the Early to Middle Pleistocene of Europe contained two canid lineages. The less derived *C. arnensis* from Upper Valdarno became *Canis* aff. *arnensis* (advanced form) and occupied the Mediterranean region, whereas the

second lineage was formed of *C. etruscus* - *C. mosbachensis*, which occupied central and northern Europe and Eurasia (Rook and Torre, 1996b).

Other Pleistocene canids also played an important role in their interactions with the wolf lineage as part of the Early and Middle Pleistocene canid guild. These include members of the genus *Cuon* (absent from Britain and not explored in this research) but which appear elsewhere in Europe by the early Middle Pleistocene (e.g. Kurtén and Poulianos, 1977; Thenius, 1954; Schutt, 1973) and chiefly, the lineage of the hypercarnivorous hunting dogs: *Canis falconeri* Forsyth-Major, 1877, *Canis* (*Xenocyon*) *lycanoides* Kretzoi, 1938, and the modern *Lycaon pictus* Temminck, 1820. *C. falconeri* was considered to be the progenitor of *C*. (*X.*) *lycaonoides* (Masini and Torre, 1990), which first occurred during the late Early Pleistocene (latest Villafranchian) at Venta Micena, Spain (Rook and Martinez-Navarro, 2010) and Pirro Nord, Italy (Petrucci *et al*., 2013). Martinez-Navarro and Rook (2003) proposed a gradual evolution of this hunting dog lineage based on anatomical, ethological and ecological characteristics, such as the gradual evolution of less derived large molars in earlier forms, into the smaller, hypercarnivorous and trenchant dentition of the modern hunting dog,. Consequently, Martinez-Navarro and Rook (2003) believed that all hunting dogs should be grouped into the genus *Lycaon*, and be represented by three chrono-species: *Lycaon falconeri* (= *C. falconeri*) for Early Pleistocene Eurasian forms, *Lycaon lycanoides* (= *C.* (*X.*) *lycaonoides*) for the remaining Early Pleistocene to early Middle Pleistocene Eurasian and African forms, and finally, *Lycaon pictus* for the Late Pleistocene and extant African form.

This was challenged by Werdelin and Lewis (2005) on the grounds that giving *Lycaon* full generic status renders *Canis* paraphyletic and they accordingly referred to the ancestral species of the lineage '*Lycaon' falconeri* as *Canis*. Hartstone-Rose et al. (2010) also considered a relatively recent origin for *L. pictus* and further addressed the nomenclature issues raised by Werdelin and Lewis (2005). If *Lycaon* and *Cuon* are accepted as valid genera (leaving *Canis* as paraphyletic), both are then representative of monophyletic clades containing some members of the genus *Canis*, while placing some species traditionally assigned to *Canis* (specifically black backed jackals and side striped jackals) outside that clade. The result would be that black backed and side striped jackals should be placed into their own genus *Lupulella* Hilzheimer, 1906 (Hartstone-Rose *et al*., 2010). The phylogenetic relationships within the Canidae itself are beyond the scope of this research. However, in light of unresolved relationships, both *C. falconeri* and *C.* (*X.*) *lycaonoides* will remain

named as such here, and both jackals will remain as *Canis mesomelas* and *Canis adustus* respectively.

3. Body Mass: an introduction

Body size plays a significant role in evolution and is one of the most important ecological factors affecting mammals, dictating ecological niche by controlling food habits, by defining prey selectivity, size and range (Gittleman, 1985), as well as shaping behavioural adaptations relating to locomotion and mode of predation. Body size is also correlated with many ecological characteristics such as life history traits, thermal biology and metabolic rate, population group size and home range size. It also correlates with the structure of the mammalian community, as competition for resources varies with the body size of the predators present, as well as the size of available prey (Gittleman, 1985; Damuth and MacFadden, 1990).

3.1. The relationship between metabolic needs and body size

The influence body size has on mammalian metabolism, activity rate, locomotor behaviour, running speed and home range size will be discussed in the following sections. By examining how size exerts control over a species, the causes of size change can be more fully elucidated.

3.1.1. Metabolism

Metabolism (the chemical processes that occur within a living organism to sustain life) is a key physiological function integral to the ecology, distribution and overall evolution of mammals (McNab, 1990). Related to metabolism is the rate of energy expenditure (basal metabolic rate), which represents the volume of oxygen metabolised per unit of body weight (Gittleman, 1985) or per hour (White and Seymour, 2003). Basal rate represents the lowest rate of a mammal's metabolism, and thus is the minimal expenditure of energy.

An allometric relationship exists between basal rate (BMR) and body mass (M), although the exact scaling of this relationship is debated as either BMR $\propto M^{2/3}$ or BMR $\propto M^{3/4}$ (Kleiber, 1932; White and Seymour, 2003). Nonetheless, mammalian metabolic rates increase with body weight (Elgar and Harvey, 1987; McNab, 1988, 1990), thus large mammals tend to have higher metabolic rates than smaller ones. However, this relationship is complex, with many taxa found by Hayssen and Lacy (1985) to have differing basal metabolic rates regardless of their body size, including differences within taxa of the

same Order. Reasons for this complexity may include the influence of diet, habitat, and activity level on basal rate, all of which relate to body mass. Mammals that specialise on either grass or vertebrates (e.g. many ungulates and carnivores) have higher basal rates than mammals of a similar weight that specialise on fruits, leaves and invertebrates (McNab, 1980, 1990). The low basal rate of the latter may be an adaptation to seasonal variation in food supply or reflect food digestibility or toxicity (McNab, 1980, 1990).

However, as all mammals are reliant on resource availability, which is often seasonal or time-dependent, adjustments to energy expenditure are common place. This adjustment is not uniform, with mammals either remaining active but modifying their energy expenditure, some migrating, and others entering a state of torpor (McNab, 1997). Basal rates are also influenced by climate and hence latitude, as high latitude Nearctic and Palaearctic mammals having higher basal rates than their Afrotropical, Indomalayan and Neotropical counterparts (Lovegrove, 2000). This relationship will be further discussed in section 3.4.

Overall, mammals maintain a metabolic rate as high as possible, one that can be sustained by the quantity and quality of resources available (McNab, 1980). Hence, for a mammal to increase in body size, an increase in the rate of energy expenditure is required, and hence an increase in the amount of food and energy available in its environment is essential (McNab, 1990).

3.1.2. Activity rate and locomotor behaviour

Basal metabolic rates are also affected by mammalian activity levels (McNab, 1980, 1990). The 'scope' of metabolism, whereby the ratio of maximum steady state rate (i.e. activity) to basal metabolic rate indicates the influence of activity on basal rate (McNab, 1980). For example, species with low basal rates (such as arboreal mammals) have either constant or decreased scope, and hence in these low activity species, activity does not change daily energy expenditure (McNab, 1980). In order for scopes to increase, muscle mass must also increase to permit higher activity levels (McNab, 1990). Higher activity requires an increase in metabolism in mammals and basal rates can be 8- to 10-fold greater for mammals during maximal aerobic activity in comparison to when resting (Nagy, 1987). Large amounts of heat are also generated as a by-product of high skeletal muscle activity (Pough *et al.,* 2002).

The activity level of a mammal can be indicated by its locomotor behaviour: arboreal, scansorial, terrestrial or semi-fossorial (Van Valkenburgh 1985, 1987). In general, terrestrial species have higher basal rates than arboreal species and higher levels of activity. In terrestrial species, particularly cursorial mammals, the energetic cost of cursoriality increases with body mass and the velocity of movement (McNab, 1990).

3.1.3. Running speed and home range size

Maximum running speed is more highly correlated to maximal rate of oxygen consumption (itself an energetically costly activity [Garland, 1983a]), as opposed to basic metabolic rate (Lovegrove, 2000). However, in highly mobile mammals such as artiodactyls, carnivores and lagomorphs, there is a relationship between fast running speeds and high metabolic rates (Lovegrove, 2000). In terms of endurance, mammals require an increased metabolic rate combined with a large aerobic capacity (increased oxygen consumption ability) (Hayes and Garland, 1995).

Maximum running speed was found to scale with body mass in most animals (Garland, 1983b; Eisenberg, 1990), although with the caveat that the largest were often not the fastest. Of note, in members of the Artiodactyla, Carnivora and Rodentia, running speed was found to be independent of body mass, with some smaller species able to run as fast as large ones (Garland, 1983b). In contrast, no scaling relationship has been noted between limb length and running ability (Garland, 1983b), since small animals are just as able to run as larger animals. It is also noteworthy that although the energetic costs of transportation are not reduced by being cursorially adapted, these adaptations may relate to performance, such as speed and endurance (Garland, 1983a), which indirectly do have an effect on metabolic rate.

Although differences were present in artiodactyls and carnivores, the energetic cost of transport in terrestrial mammals generally increases with body mass (Garland, 1983a). As a result, large mammals were predicted to move greater distances for foraging, and hence have larger home ranges than small mammals, based on their higher energetic needs (Garland, 1983a; Gittleman and Harvey, 1982; Eisenberg, 1990). Home range size is influenced by many other factors, including activity level and locomotory behaviour, predation risk, diet and food consumption, as well as stomach capacity (Garland, 1983a; Gittleman and Harvey, 1982; Lovegrove, 2000). In carnivores, home range size increases with metabolic need, often related to the changing needs of the group (Gittleman and

Harvey, 1982). The relationships between body size, prey and home range size will be further discussed in the next section.

3.2. Relationship between diet, body size and community structure

Interactions between body mass and metabolism, activity rate, locomotor behaviour, running speed and home range size are therefore complex, determining diet, prey choice and competition, and ultimately influencing carnivore community structure.

3.2.1. Diet, prey choice and body size

In carnivores, body size directly influences the ability to chase, apprehend and kill prey of a particular size (Gittleman, 1985). Carbone et al. (1999) identified a dietary shift in carnivores between 21.5-25kg. For carnivores with body masses below 21.5Kg, selected prey was less than half the size of the predator and diet was likely to be more omnivorous, whereas above this threshold, prey was similar to or larger than the predator and diets were more carnivorous (Carbone *et al.,* 1999). Energetic constraints were suggested to be the most influential factor on dietary threshold (Carbone *et al.*, 1999), although Andersson (2004b) implicated both metabolic rate and energy expenditure, rather than body size. As discussed previously, factors responsible for the dietary threshold are likely multiple and complex.

Larger mammals need larger home ranges due to their increased energetic requirements. Carnivore home range size is often determined by migratory prey (Gittleman and Harvey, 1982), as well as hunting success. Both wild dogs and wolves will search their home range extensively for prey, yet in times of abundance, ranges are reduced (Gittleman and Harvey, 1982). Thus, large home ranges in carnivores increase the chances of finding food (Garland, 1983a; Gittleman, 1985).

Large size and mobility in carnivores enable the pursuit of larger and faster prey (Gittleman, 1985). In addition, carnivores that have retained the ability to supinate their forearms and are therefore able to grapple with prey (such as bears) tend to increase in body mass. In contrast, those that have developed pursuit hunting remain modestly sized, with cursors rarely reaching 100kg (Andersson and Werdelin, 2003; Andersson, 2004b). Carnivores of less than 20kg can remain intermediate between hunting modes, whereas those above this

threshold are committed to one or the other of the pathways (Andersson and Werdelin, 2003).

Beyond this hunting mode threshold, there is a strong pressure to increase body mass up to and above 40kg, which were related by Andersson (2004b) to the energetic costs of locomotion. A 'cursorial window' at 40-80Kg was identified, since the longer strides of larger animals will be more energy efficient than those of smaller animals (Andersson, 2004b).

The interactions between body size, hunting and diet are complex. As highlighted by Carbone et al. (1999), larger carnivores above the dietary threshold are distinct and not simply 'scaled-up versions' of smaller carnivores. The same applies to the hunting mode threshold, emphasising that larger carnivores are different both ecologically and physiologically.

3.2.2. Body size, carnivore community structure and competition

The relationship between body size and community structure is equally complex and only a summary can be made here, in view of the volume of research published and its importance to understanding ecological interactions.

The ecology of a community relates to its composition and organisation (Begon *et al.*, 2006). Hence, community structure reflects how a group of species is distributed in an area and how they coexist. Many factors affect community structure, including how energy is acquired and appropriated, interactions between coexisting species, body size, foraging habits and diet (Hutchinson, 1959; Brown, 1981; Marti *et al.*, 1993; Begon *et al.*, 2006; Rodriguez, 2006). The type of habitat available determines the ecological roles available in a community (Begon *et al.*, 2006). The differentiation of roles among species reflects differences in their morphology, physiology and environmental responses (Begon *et al.*, 2006). Thus, the ecological niche of a species is multidimensional, including the summation of its tolerances and requirements, as well as how it interacts with other coexisting species. Interspecific interactions (often through competition) are frequently considered to be a structuring 'force' in a community, ultimately dictating the partitioning of space and resources (Marti *et al.*, 1993).

Where two closely-related species are sympatric, they often develop more pronounced differences through character displacement than when they are geographically separated

(Brown and Wilson, 1956). In light of this relationship, character displacement is often used as evidence for competition, and thus for inferences on community structure (Dayan and Simberloff, 2005; Garcia and Virgos, 2007). Based on the character displacement theory of Brown and Wilson (1956) that ecologically similar species cannot coexist and that size divergence occurs when formerly allopatric species enter sympatry and hence competition, Hutchinson (1959) established size ratios that differentiated between two coeval species at similar trophic level. These ratios identified a minimum size difference in closely-related species, as reflected in the dimensions of their trophic apparatus (e.g. skull length in mammals). Thus when species co-occur, the minimum size difference creates space in the community by differentiating between them, thereby enabling species to coexist in different ecological niches but at the same trophic level (Hutchinson, 1959).

Ultimately, any divergence in size and shape of similar species potentially reduces resource overlap and thus interspecific competition (Dayan and Simberloff, 2005). However, the morphological traits involved in character displacement must be of functional significance for differences to evolve in response to competition and resource partitioning (Dayan and Simberloff, 2005). Thus a strong relationship exists between morphology (such as specialised dentition) and resource partitioning, which in turn relates to the relationship between morphology and ecological niche established earlier.

As already discussed, there is a close relationship between predator and prey size. With respect to competition and community structure, the ratio of predators to prey is often a mechanism for controlling diversity within a community (Raia *et al.*, 2007). Predator-prey size ratios are therefore used to determine ecological balance in a community (Garcia and Virgos, 2007; Raia *et al.,* 2007), based on being either predator-limited or food-limited. Predators in a community tend to enhance species richness, for example where community productivity is high and the preferred prey is overly abundant, predators will regulate prey numbers in the community (Begon *et al.*, 2006).

Top predators can influence community structure by having a 'top-down' effect, whereby they are indirectly responsible for regulating plant and lower animal communities (Gompper, 2002). Case studies from modern North American *C. lupus* provide a prime example of this effect, for example, wolves indirectly promoting tree growth by regulating moose numbers in Isle Royale (Post *et al.*, 1999) and elk in Yellowstone National Park (Ripple *et al.,* 2001; Fortin *et al.,* 2005).

3.2.3. Body size and Cope's rule

The ecological niche of a species is largely determined by its tolerances and requirements but there is also an optimum body size for the niche a species occupies (Stanley, 1973). For example, for a species to fill a certain niche, an initial increase in size may be advantageous. However, once the optimum body size has been reached, any further increase will become disadvantageous. Nevertheless, because of the variability of climate and environmental conditions, ecological niches and optimum sizes are necessarily flexible (Stanley, 1973).

The tendency of animal groups to evolve towards larger body size over time is the main thesis of Cope's rule (Stanley, 1973; Alroy, 1998; Benton, 2002). Cope's rule is based on there being certain advantages to size increase, such as an improved ability to capture prey or ward off other predators, greater reproductive success, increased intelligence (with increased brain size), as well as being able to exploit a wider range of food types and having extended individual longevity (Stanley, 1973; Hone and Benton, 2005). Thus, when an evolutionary size increase occurs, it is usually linked to one or more of these advantages (Stanley, 1973).

3.3. Sexual size dimorphism

Sexual dimorphism is the difference in size and shape between males and females of the same species. Based on the higher energetic demands of female mammals related to egg production, gestation and lactation, females would expected to be larger than males (Darwin, 1871; Lindenfors *et al.*, 2007) but the reverse is often true in many birds and mammals (Clutton-Brock *et al.*, 1977; Lindenfors *et al.*, 2007).

In mammals, male-biased sexual size dimorphism is often explained by sexual selection favouring larger, more competitive males in sexually-driven contests between males for females (Clutton-Brock *et al.*, 1977; Isaac, 2005). The level of sexual size dimorphism varies by Order, with the most extreme differences occurring in Primates (baboons, orang-utan and gorilla), Pinnipedia (fur seals, sea lions, elephant seals) and Proboscidea (African elephant) (Ralls, 1977). However, sexual selection alone does not account for the variation in sexual dimorphism found in mammals and is likely the result of a combination of factors (Ralls, 1977; Isaac, 2005), one of which is the level of parental investment from males. In species where males have a large investment in offspring, low levels of dimorphism are more often apparent (Ralls, 1977). Of these, monogamous species generally have a larger

investment in offspring in comparison to non-monogamous species. Thus, breeding system is often also related to the variability found in sexual dimorphism (Ralls, 1977). Interestingly, the defence of both young and of territory may be more correlated with dimorphism, since larger size is more advantageous in conflict and sexual dimorphism is more pronounced in those species that defend young and territory (Ralls, 1977).

Sexual dimorphism also manifests itself in secondary sexual characteristics often used in display and as weapons, such as canine teeth (Ralls, 1977; Gittleman and Van Valkenburgh, 1997). Here, non-monogamous males have more dimorphic canines than monogamous ones (Gittleman and Van Valkenburgh, 1997). In summary, sexual size dimorphism varies by taxon, parental investment and breeding system. It also varies by species body size, with extreme dimorphism more frequent in large mammal species than in smaller ones (Ralls, 1977).

This relationship between body size and sexual dimorphism has been related to Rensch's rule (Rensch, 1960), whereby sexual size dimorphism is positively correlated with mean body size in taxa where males are the larger sex, yet is negatively correlated with mean body size in taxa within which females are the larger sex (Abouheif and Fairbairn, 1997).

3.4. The relationship between body size, temperature, latitude and climate

The relationship between body size, ambient and body temperature, latitude and climate will be explored in the following sections.

3.4.1. Temperature, body mass and metabolic rate

As mentioned above, body mass and metabolic rate are interlinked, with larger mammals tending to have higher metabolic rates than smaller ones. However, the effect of temperature also has a role, since it governs metabolism via its effect on biochemical reactions (Gillooly *et al.*, 2001). Generally, metabolic dependence on temperature has a limited range between 0-40°C, within which most organisms operate under natural conditions. For example, at around 0°C metabolic reactions cease because of water freezing, whilst at and above 40°C, metabolic reactions reduce due to the increasing effect of catabolism (the rate at which molecules are broken down) (Gillooly *et al.*, 2001).

Regulation of body temperature (i.e. thermal conductance, the ability to transfer heat) and basal metabolic rate both vary, and are related to body mass. As indicated by McNab (1970), temperate-climate species generally have higher basal rates for their weight, but only demonstrate a slight increase in conductance, unless they are of very large size. They therefore have precisely regulated and high body temperatures, related to living in thermally unstable environments (McNab, 1970).

In contrast, many desert mammals, such as rodents, have low basal rates and high conductance to reduce risk of over-heating (McNab, 1970). Tropical species also have low basal rates but frequently poor thermal regulation, their resultant low body temperatures only tolerable because they inhabit thermally stable environments (McNab, 1970). Thus climate is an important factor in both metabolic rate and body temperature.

3.4.2. Body size, latitude and climate

Climate has been established above as an important driver in temperature regulation and basal metabolic rate in mammals. Both ambient temperature and latitude are involved, with a decrease in temperature correlated with increasing latitude (Mayr, 1963), and both are correlated with body size (Rosenweig, 1968).

This relationship forms the basis of Bergmann's rule, which states that warm-blooded mammals from cooler climates tend to be larger than their congeners from warmer climates (Bergmann, 1847). This rule was subsequently re-formulated to refer to populations within species. Thus, within a given species of homeotherms, populations living in colder climates are generally larger than populations living in warmer climates (Rensch, 1938; Mayr, 1963).

As mentioned earlier, animals in colder climates tend to have higher basal rates than those in warm climates (McNab, 1990; Lovegrove, 2000), reflecting the need for increased energy consumption. Animals with higher basal rates also tend to be larger, and hence part of the reasoning behind Bergmann's rule is that large animals expend less energy for thermoregulation due to their smaller surface-to-volume ratio (McNab, 1971). Heat production is related to an animal's volume, whereas heat loss is related to its surface area. Hence, large animals in cold climates are at an advantage since they tend to produce more heat and lose relatively less, compared to smaller animals (Meiri and Dayan, 2003).

The validity of Bergmann's rule, however, is contentious, with multiple other factors invoked to explain why increases in body size occur in cold climates. For instance, latitudinal changes in food or prey size and an increase in competition or seasonality were preferred by Gittleman (1985) for explaining large size at high latitude. Bergmann's rule has also been considered as an exceptional occurrence within the general trend of predator body size being controlled by the distribution of prey and the presence of other predators (McNab, 1971). However, many examples exist that uphold the rule and it can be used as a generalisation for most mammals and birds (Ashton *et al.,* 2000; Meiri and Dayan, 2003).

3.5. Summary

In summary, body size is influenced by, and directly connected to, many important variables, highlighting both the power body size has over much of an animal's ecology and biology, and how external factors such as climate influence it. A detailed investigation of body size in the Pleistocene canids was therefore undertaken in the present study, with the aim of further understanding how differences in size affected them, as well as how changes in size reflected on the whole mammal community.

4. Materials, methods and rationale for approach

The following sections outline the materials examined, the rationale behind the analysis, and the methods used in order to address, in part, the research aims of how body mass and ecology have changed within and between the four Pleistocene canids over time.

4.1. Materials

Total number of Pleistocene canid specimens recorded (NISP) was 5604, of which *C. lupus*: 4621, *C. mosbachensis*: 666, *C. arnensis*: 95, and *C. etruscus*: 222 (see Tables 5.1, 5.2). In total this represented (based on MNI) 122 individuals of *C. lupus*, 46 individuals of *C. mosbachensis*, 8 individuals of *C. arnensis* and 21 individuals of *C. etruscus* (also see Table 5.1, 5.2). Additionally, a total of 235 individuals of modern canids were recorded (see later).

For the canid material studied here, species assignations were taken from the literature and accepted as accurate. Personal observations of morphology were also recorded (see section 2.3) during the measuring of specimens in museum collections to cross-check existing identifications.

Figure 4.1 and 4.2 shows the location of the sites studied in the present research. Details of the localities are tabulated below, including beds that have produced canid remains, palaeoenvironmental and palaeoclimatic significance and indications of age. Table 4.1 lists the sites studied in Britain, whereas Table 4.2 lists the sites from continental Europe, together with the museum collections where remains are housed. Selected specimens are shown in Figures 4.3 and 4.4. Individual species lists from all study sites are provided in Appendix 1.

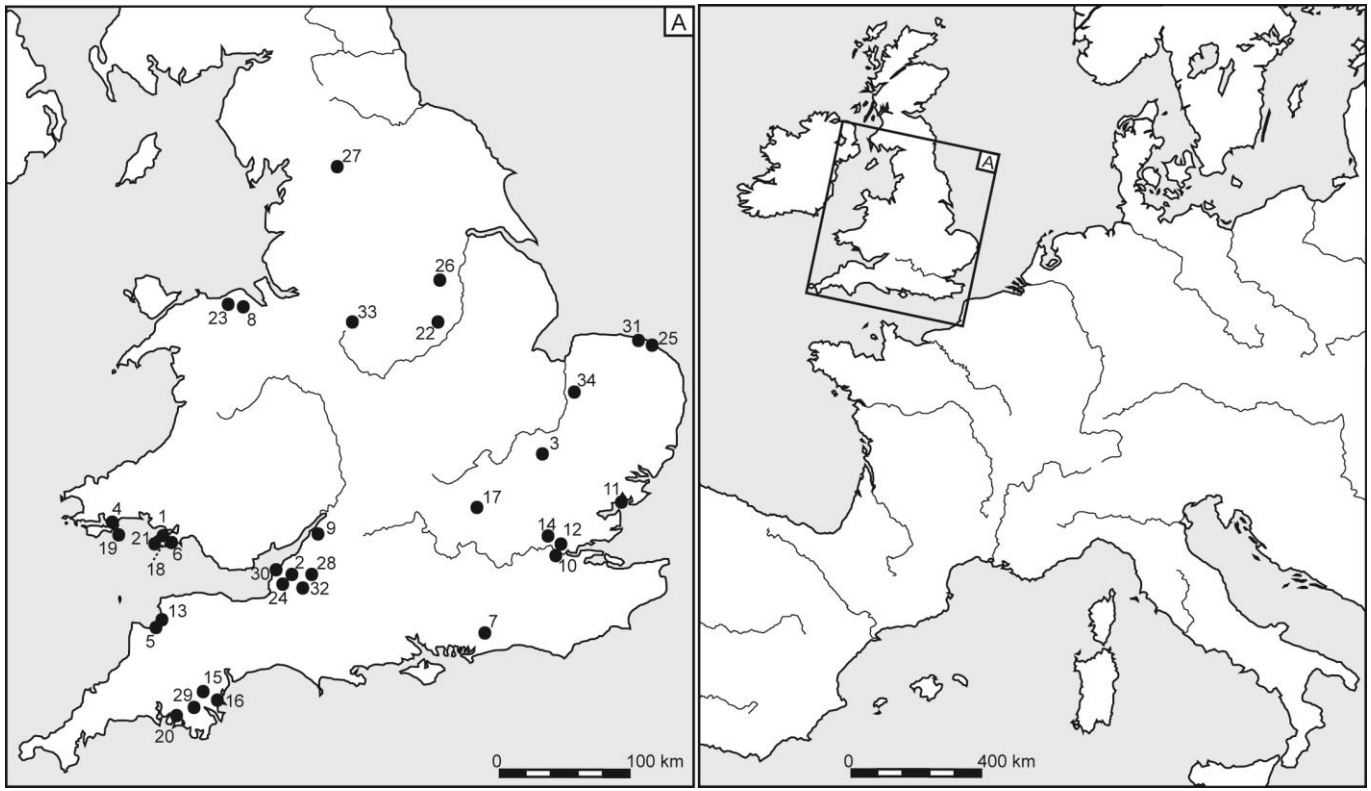


Figure 4.1 Map of northwest Europe. **A**: detailed map of Britain illustrating sites used in the analyses. Sites indicated in Britain: 1: Bacon Hole, 2: Banwell Bone Cave, 3: Barrington Beds, 4: Black Rock Quarry, 5: Bleadon Cave, 6: Bosco's Den, 7: Boxgrove, 8: Cae Gwyn Cave, 9: Clevedon Cave, 10: Crayford, 11: Cudmore Grove, 12: Grays Thurrock, 13: Hutton Cave, 14: Ilford, 15: Joint Mitnor Cave, 16: Kents Cavern, 17: Marsworth, 18: Minchin Hole, 19: Ogof yr Ychen, 20: Oreston Cave, 21: Paviland, 22: Pin Hole Cave, 23: Pontnewydd Cave, 24: Sandford Hill, 25: Sidestrand, 26: Steetley Quarry Cave, 27: Stump Cross Cave, 28: Sun Hole, 29: Tornewton Cave, 30: Uphill Quarry, 31: West Runton, 32: Westbury-sub-Mendip, 33: Windy Knoll, 34: Wretton.

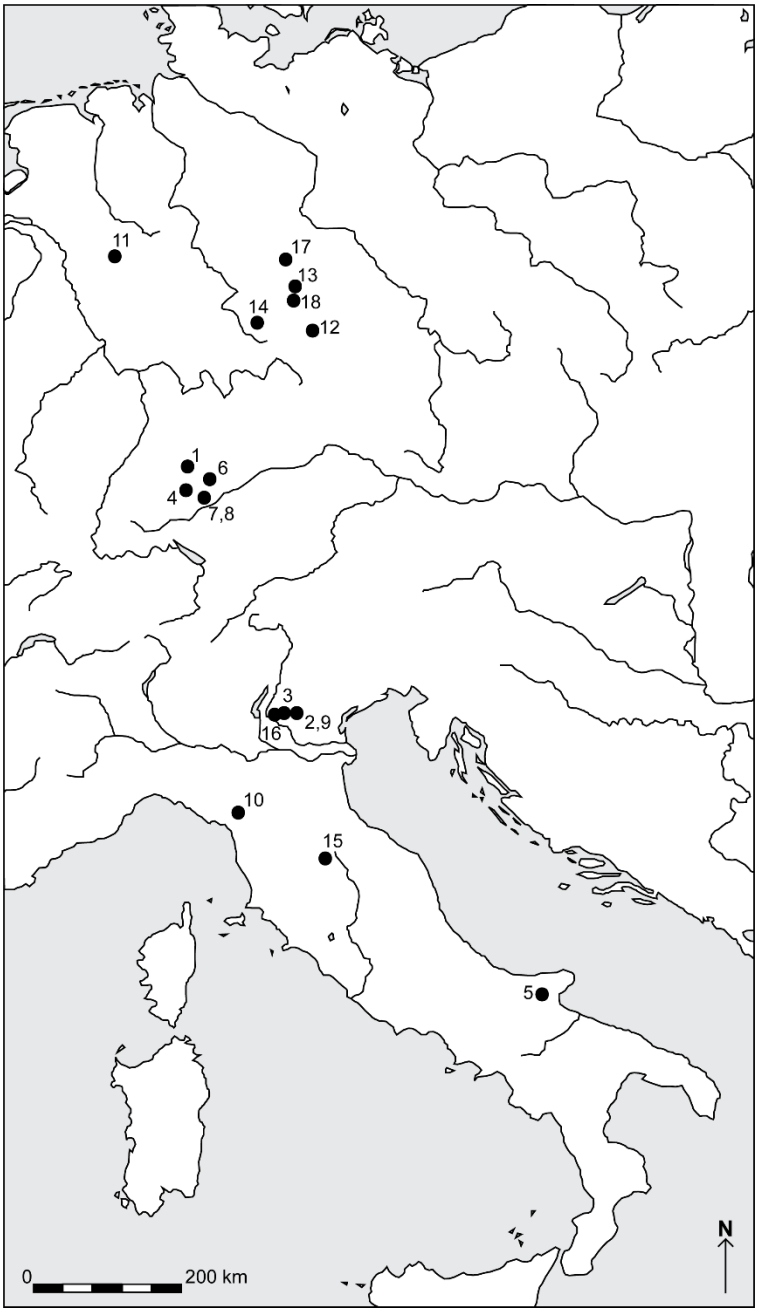


Figure 4.2. Map of central and southern Europe including Germany and Italy illustrating sites used in the analyses. Sites indicated: 1: Bad Canstatt (Villa Seckendorf), 2: Castello, 3: Cengelle II, 4: Dobelhaldeschacht, 5: Grotta Paglicci, 6: Heppenloch, 7: Hohle Fels, 8: Kogelstein, 9: Monte Zoppega, 10: Olivola, 11: Perick Cave, 12: Ranis, 13: Taubach, 14: Untermassfeld, 15: Upper Valdarno Basin, 16: Viatelle, 17: Voigtstedt, 18: Weimar-Ehringsdorf.

	Locality	Beds yielding canid material	Climate/Palaeoenvironment	Age	Canids present	Sources	Coll.
Early Middle Pleistocene	West Runton, Norfolk; TG 188432/TG 185432	West Runton Freshwater Bed	Temperate (peak summer temperatures 16-19°C, peak winter temperature -3 to 5°C). Mixed woodland	MIS 17	*C. mosbachensis* (small *C. lupus* of Stuart, 1995)	West 1980; Stuart, 1995; Coope, 2010; Maul & Parfitt, 2010	NHM
	Westbury-sub-Mendip, Somerset; ST 506504	Calcareous Member units: 2 12, 13, 14 18, 19/14, 19/15, 19 (W1A), 19, Bed 4a	 Temperate Cooler Temperate	MIS 13	*C. mosbachensis** *C. (X.) lycaonoides*	Bishop, 1974, 1982; Andrews & Cook, 1999 Schreve *et al*., 1999 Preece & Parfitt, 2000	NHM, BC UBSS
	Boxgrove, West Sussex; SU 918087/SU 924085	unit 4b silts & clays unit 4c land surface unit 5a organic bed unit 5b marl unit 6 silt	Mixed woodland Grassland/scrub, nearby water Increasingly boreal & cool Open environment, cool temperate Cool with increasing woodland	MIS 13	*C. mosbachensis**	Roberts & Parfitt, 1999; Parfitt, 1999; Preece & Parfitt, 2000	NHM
	Sidestrand, Norfolk; TG 263395	Sidestrand Hall Member ('*Unio* Bed')	Warm (summer temperatures 16-24°C, winter temperatures +9 to -9°C); mixed woodland/open grassland with fresh water and marsh	MIS 13	*C. mosbachensis*	Preece *et al*., 2009	NHM
Late Middle Pleistocene	Cudmore Grove, Essex; TM 068146	Detrital muds	Summer temperatures 17-18°C, woodland, water source present	MIS 9, Purfleet MAZ	*C. mosbachensis*	Schreve, 2001a; Roe *et al*., 2009	NHM
	Grays Thurrock, Essex	Laminated clays with sand and gravel layers, overlain by shell bed	Warm, predominantly forested with open grassland adjacent to river	MIS 9, Purfleet MAZ	*C. mosbachensis*	Dawkins, 1867	NHM
	Pontnewydd Cave, Denbighshire	Lower Breccia Intermediate Complex	Temperate, mixed woodland/open grassland, presence of a water source	MIS 7, 225+89/-47 Ka	*C. lupus*	Green *et al.,* 1981; Currant, 1984; Schwarcz, 1984; Campbell & Bowen, 1989	NMW

	Bleadon Cave, Somerset ST 36065813	Ochreous cave earth	Temperate, mixed woodland/grassland	MIS 7a, Sandy Lane MAZ	*C. lupus*	Schreve, 1997, 2001a, Currant, 2004; Candy & Schreve, 2007	NHM, SHC
	Hutton Cave, Somerset	Ochreous cave earth	Temperate, open grassland	MIS 7a, Sandy Lane MAZ	*C. lupus*‡	Currant, 2004; Schreve, 1997, 2001a	NHM, SHC
	Tornewton Cave	Otter Stratum; broken stalagmite floor & sediment	Woodland, presence of water source	MIS 7, 224 Ka, Ponds Farm MAZ?	*C. lupus*	Procter & Smart, 1996; Schreve, 1997, 2001a; Currant, 1998	NHM
	Ilford (Uphall Pit), TQ 436856	Clayey 'brickearth'	Mixed woodland & grassland, temperate	MIS 7, Sandy Lane MAZ	*C. lupus*	Schreve, 1997, 2001a	BGS
	Marsworth, Buckinghamshire, SP 933143	Lower channel; organic muds, fossiliferous gravelly sands	Warm, woodland & grassland	MIS 7a, 209 Ka BP. Sandy Lane MAZ	*C. lupus*	Green et al., 1984; Murton et al., 2001; Schreve, 2001a, Candy and Schreve, 2007	BCM
	Crayford, Kent, TQ 517758	Sand & clay 'brickearth'	Temperate, steppe grassland	MIS 7, Sandy Lane MAZ	*C. lupus*	Spurrell, 1880; Kennard, 1944; Schreve, 2001a	BGS, NHM
	Clevedon Cave, Somerset, ST 41847265	Fossiliferous cave earth & gravel beds	Cold, steppe grassland	MIS 6	*C. lupus*	Reynolds, 1907; Currant & Jacobi, 2011	BC, BGS
Late Pleistocene	Barrington Beds, Cambridgeshire, TL 381491/TL 406498	Grey gravelly silt containing shells and vertebrate remains	Fully interglacial, above freezing mean winter temperatures. Woodland, with water source nearby	MIS 5e, Joint Mitnor Cave MAZ	*C. lupus*	Gibbard & Stuart, 1975; Currant & Jacobi, 2001	NHM, SMES
	Joint Mitnor Cave, Devon, SX 744665	Fossiliferous cave earth	Fully interglacial, warmer than present temperatures, woodland with water source nearby	MIS 5e, 120 ±6Ka, Joint Mitnor Cave MAZ	*C. lupus*	Gascoyne et al., 1981; Campbell & Stuart, 1998; Currant & Jacobi, 2001	NHM, TM
	Bacon Hole, Gower, SS 56058683	Unit I: Upper cave earth Unit G: Grey clays, silts and sands	Climatic cooling. Mixed woodland/open grassland	MIS 5c, 87.22 +1.99/-1.78 Ka, Bacon Hole MAZ	*C. lupus*	Currant & Jacobi, 2001, 2011; Gilmour et al., 2007	NHM, SM

	Minchin Hole, Gower, SS 54688730	Unit 8: Earthy breccia series Unit 7: *Neritoides* beach	Climatic cooling, change from woodland to more open grassland environments	MIS 5c, Bacon Hole MAZ	*C. lupus*	Sutcliffe *et al*., 1987; Curant & Jacobi, 2001, 2011	SM
	Banwell Bone Cave, Somerset, ST 383588	Bone deposit	Cold, open tundra	MIS 5a, Banwell Bone Cave MAZ	*C. lupus*‡	Currant & Jacobi, 2001; Curant, 2004	BC, BGS, NHM, SHC, UBSS
	Bosco's Den, Gower, SS 55918684	Bed 8: sandy loam Bed 3: cave earth	Cold, open tundra	MIS 5a, Banwell Bone Cave MAZ	*C. lupus*	Campbell & Bowen, 1989; Currant & Jacobi, 2001	NMW, SM
	Steetley Quarry Cave, Nottinghamshire, SK 553790	Fissure filling	Cold, tundra	MIS 5a, Banwell Bone Cave MAZ	*C. lupus*	Currant & Jacobi, 2001; Pike *et al*., 2005; Gilmour *et al*., 2007	WH
	Stump Cross Cave. North Yorkshire, SE 089634	Detrital layer between stalagmite flowstones	Cold, tundra	MIS 5a, 73.86 +1.2/-1.19 Ka, Banwell Bone Cave MAZ	*C. lupus*	Currant & Jacobi, 2001; Gilmour *et al*., 2007	NHM
	Windy Knoll, Derbyshire	Yellow clay deposit	Cold, tundra	MIS 5a, Banwell Bone Cave MAZ	*C. lupus*	Dawkins, 1877; Currant & Jacobi, 2001	BM, MM
	Wretton, Norfolk	Organic deposit	Cold tundra	MIS 5a, Banwell Bone Cave MAZ	*C. lupus*	Sparks & West, 1970; Stuart, 1977; Murton *et al*., 2001	UMZC
	Black Rock Quarry, Pembrokeshire, SN 109002	Unknown, site lost	Cool conditions, steppe grassland	MIS 3	*C. lupus*	Dawkins, 1874; Davies, 1989	SMES
	Kents Cavern, Devon, SX 934642	Cave earth	Cool conditions, steppe grassland	MIS 3, range 35,150 ±330 – 37, 200 ±550, Pin Hole Cave MAZ	*C. lupus*	Keen, 1998; Procter *et al.*, 2005	MM, NHM, TM
	Oreston Cave, Devon	Clay deposit	Cool conditions, steppe grassland	MIS 3, Pin Hole Cave MAZ	*C. lupus*‡	Clift, 1823; Whidbey, 1823; Boylan, 1981; Currant & Jacobi, 2001	BCM, NHM, WH

	Paviland (Goat's Hole), Gower, SS 43738588	Unknown. Main passage, area F	Cool conditions, steppe grassland	MIS 3, 42,650 ±800 – 15,250 ±120, Pin Hole Cave MAZ	*C. lupus*‡	Currant & Jacobi, 2001; Jacobi & Higham, 2008	NHM, NMW, SM
	Pin Hole Cave, Derbyshire, SK 533742	Cave earth	Cool, steppe grassland	MIS 3, 41,900 ±900Ka - 55,900 ±4000, Pin Hole MAZ	*C. lupus*	Jacobi *et al*., 1998; Currant & Jacobi, 2001; Jacobi *et al*., 2009	MM
	Sandford Hill, Somerset, ST 422591	Cave earth	Cool, steppe grassland	MIS 3, 36,000 ±1900Ka, Pin Hole MAZ	*C. lupus*	Burleigh et al., 1982; Currant, 2004	SHC
	Uphill Quarry, Somerset	Fossiliferous deposit, cave 7 or 8	Cool, steppe grassland	MIS 3, 31,730 ±250Ka	*C. lupus*	Wilson & Reynolds, 1902; Harrison, 1977; Jacobi, 2000	BC
	Cae Gwyn Cave, Clwyd, SJ 085724	Red laminated clay and bone earth	Cool, steppe grassland	MIS 2, 18,000 +1400/-1200, Dimlington Stadial MAZ	*C. lupus*	Rowlands, 1971; Campbell & Bowen, 1989	NHM
	Ogof yr Ychen, Caldey Island, SS 14649691	Yellow silty clay	Cool, steppe grassland	MIS 2, 22,350 ±620 Ka, Dimlington Stadial MAZ	*C. lupus*	Bateman, 1973; van Nedervelde et al., 1973; Davies, 1989	NMW
	Sun Hole, Somerset, ST 467541	Unit 1: layers 1-13	Cool to cold, steppe grassland	MIS 2, 12,755 ±55Ka, Gough's Cave MAZ	*C. lupus*	Collcutt *et al*., 1981; Currant & Jacobi, 2001, 2011	UBSS

Table 4.1. Sites studied in the present research, outlining beds of interest (NB only those yielding canid material are presented), with climatic and palaeoenvironmental summary, inferred age and mammal assemblage zone (MAZ), species present, key sources and location of collections visited. *denotes specimens figured in Figure 4.3. ǂ denotes specimens figured in Figure 4.4. Abbreviations for collections as follows: Bristol City Museum (BC), British Geological Survey, Keyworth (BGS), Buckinghamshire County Museum (BCM), Manchester Museum (MM), Natural History Museum in London (NHM), National Museum Wales, Cardiff (NMW), Sedgwick Museum of Earth Sciences, Cambridge (SMES), Somerset Heritage Centre, Taunton (SHC), Swansea Museum (SM), Torquay Museum (TM), University of Bristol Spelaeological Society (UBSS), University Museum of Zoology, Cambridge (UMZC), Wollaton Hall (WH), Nottingham (WH). For detail on the Middle Pleistocene MAZ see Schreve (2001a), for the late Pleistocene MAZ see Currant and Jacobi (2001, 2011).

	Locality	Beds yielding canid material	Climate/Palaeoenvironment	Age	Canids present	Sources	Coll.
Early Pleistocene	Val di Magra, Tuscany, Italy	Fossiliferous breccia	Warm interglacial conditions, mosaic landscapes of grassland/woodland	Just older than c.1.8Ma, Olivola F.U.	*C. etruscus**	Forsyth Major, 1890; Azzaroli, 1983; Gliozzi *et al.,* 1997; Rook & Martinez-Navarro, 2010	IGF
	Upper Valdarno basin; Il Tasso and Faella	Fluvio-lacustrine	Cooling conditions, mean annual temperature 17.36°C, expansion of grassland	Younger than c. 1.8Ma, transition Olivola and Tasso F.U., correlated to top of Oludvai Subchron, Tasso F.U.	*C. etruscus, C. arnensis*, C. falconeri*	Azzaroli *et al.*, 1988; Rook *et al.*, 2013	IGF
	Untermassfeld, Thuringia, Germany	Fluviatile sands (upper & lower units)	Mean summer temperatures of 17-18°C, mean winter temperatures above freezing. Mosaic landscapes; grassland, woodland, water source	Just older 1Ma, correlated to base of Jaramillo event	*C. mosbachensis*, C. (X.) lycaonoides*	Kahlke, 2000; Kahlke & Gaudzinski, 2005; Kahlke *et al.*, 2011	IQW
	Viatelle, Veneto, Italy	Bone bed deposit	Temperate, woodland	Early Pleistocene	*C. l. mosbachensis*	Bon *et al.*, 1991; Montuire & Marcolini, 2002	MCSN
Early Middle Pleistocene	Voigtstedt, Thuringia, Germany	Fluvial sands, from a limnic horizon	Mean summer temperatures of 17-18°C. Woodland with water source nearby	MIS 17, correlated to West Runton	*C. mosbachensis*	Stuart, 1975, 1981; Maul & Parfitt, 2010; Stuart & Lister, 2010; Wagner *et al.*, 2011	IQW
	Heppenloch, Baden-Wurttemberg, Germany	Bone breccia	Temperate, grassland	MIS 11	*C. lupus* (Adam, 1975), but small size comparable to *C. mosbachensis*	Adam, 1975; Kahlke *et al.*, 2011	STNS
	Monte Zoppega I, Soave, Italy	Unknown	Temperate, woodland	MIS 11, Mindel-Riss (Hoxnian)	*C. mosbachensis*	Bon *et al.*, 1991	MCSN
	Castello, Soave, Italy	Unknown	Grassland/woodland	Early to Middle Pleistocene	*C. lupus* aff. *mosbachensis*	Bon *et al.*, 1991; R. Sardella (Pers. Comm,	MCSN

						2012)	
	Cengelle II, Soave, Italy	Fossiliferous 'breccia di Soave'	Grassland/woodland, water source nearby	Middle Pleistocene	*C. lupus,* small size comparable to *C. mosbachensis*	Bon *et al.*, 1991; R. Sardella (Pers. Comm, 2012)	MCSN
Late Middle Pleistocene	Weimar-Ehringsdorf, Germany	Upper Travertine Lower Travertine	Temperate, grassland Temperate, woodland	Late MIS 7, Lower Travertine: 230 Ka, Upper Travertine 111 ±47 Ka	*C. lupus*	Blackwell & Schwartz, 1986; Kahlke, 2002; Schreve & Bridgland, 2002	IQW
	Dobelhaldeschacht, Baden-Wurttemberg, Germany	Unknown cave deposit	Grassland/woodland	Late Middle Pleistocene, end of Riss glaciation	*C. lupus*	Ohmert, 1988; Rathgeber, 2008a, 2008b	STNS
Late Pleistocene	Taubach	Humic travertine sands, 'knochensanden' bone sand	Warm, grassland/woodland	Eemian, likely MIS 5e, 116 ±19 Ka	*C. lupus*	Kahlke, 1977; Brunnacker *et al.*, 1983; Kahlke, 2002; van Kolfschoten, 2000	IQW
	Bad Canstatt (Villa seckendorf), Stuttgart, Germany	Travertine	Cool, grassland/woodland	MIS 5e-c	*C. lupus*	Ziegler, 1996; Wenzel, 1998; van Kolfschoten, 2000	STNS
	Hohle Fels, Ach Valley, Swabian Alps, Germany	Clayey-silt with limestone rubble	Steppe grassland	MIS 3, 30-31 ^{14}C Ka BP	*C. lupus*	Conard & Bolus, 2008; Munzel *et al.*, 2011	STNS
	Kogelstein, Ach Valey, Swabian Alps, Germany	Cave deposit	Cool, steppe grassland	MIS 3	*C. lupus*	Munzel & Conard, 2004	STNS
	Perick Cave, Sauerland Karst, Germany	Fossiliferous bone gravel	Cool, steppe grassland/taiga forest	MIS 3, Weicheslian	*C. lupus*	Dietrich, 2009	NHM
	Ranis (Ilsenhöhle), Thuringia, Germany	Unknown, zones 2-4	Cool, steppe grassland	MIS 3	*C. lupus*	Muller-Beck & Workman, 1968	IQW
	Grotta Paglicci, Puglia, Italy	Sand, 26 layers	Grassland/woodland	MIS 2, layers 2a-18b: 23,836-13,355 Cal. ^{14}C yrs BP	*C. lupus*	Borgognini Tarli *et al.,* 1980; Delgado-Huertas *et al.*, 1997; Iacumin *et al.,* 1997	MCSN

Table 4.2. Sites studied in the present research, outlining beds of interest (NB only those yielding canid material are presented), with climatic and palaeoenvironmental summary, inferred age, species present, key sources and location of collections visited. Asterisk (*) denotes a specimen figures in Figure 4.3. Abbreviations for collections as follows: Museo di Storia Naturale degli Studi di Firenze, Italy (IGF), Senckenberg Forschungsstation für Quartäpaläontologie Weimar (IQW), Museo Civico Storia Naturale, Verona (MCSN), Natural History Museum in London (NHM), Staatliches Museum für Naturkunde Stuttgart (STNS).

Figure 4.3. Photographs of a). *C. etruscus* incomplete cranium (IGF 4407) from Olivola. Scale: 1cm, b). *C. arnensis* cranium (IGF867 type specimen) from the Upper Valdarno. Scale: 2cm, c). *C. mosbachensis* left mandible ramus (NHM M33940) from Westbury sub Mendip. Scale: 2cm, d). *C. mosbachensis* left mandible ramus (NHM F2+3/2) from Boxgrove. Scale: 1cm, e). *C. mosbachensis* right mandible (IQW 1980/15308 [Mei. 14820]) from Untermassfeld. Scale: 2cm.

Figure 4.4. Photographs of f). *C. lupus* right mandible (TTNCM 42/1995/738) from Hutton Cave. Scale: 1 cm, g). *C. lupus* left partial mandible ramus (TTNCM 40/1995/46) from Banwell Bone Cave. Scale: 2 cm. Note the presence of severe tooth wear (discussed further in Chapter 7), h). *C. lupus* right mandible ramus (NHM 46981) from Oreston Cave. Scale: 1cm, i). *C. lupus* left mandible ramus (SM 1836.6.305.1) from Paviland. Scale: 1cm.

A database of modern wolves (Table 4.3) was also compiled for comparison with fossil canids, drawn from specimens in the Natural History Museum (NHM, Zoology department) and the Naturhistoriska riksmuseet (NRM) in Stockholm, Sweden.

Inst.	Country	Species	Spec.	Sex	Est. Latitude
NHM	Riocalado, Burgos, Spain	*C. lupus*	11.10.5.1	M	42°20'38.27"N
NHM	Seville, Spain	*C. lupus*	95.3.3.6	M	37°23'17.15"N
NHM	Dolha, Poland	*C. lupus*	34.6.28.47	M	52° 0'15.42"N
NHM	Norbotten, Sweden	*C. lupus*	28.5.4.1	M	67°15'7.34"N
NHM	Moscow district, Russia	*C. lupus*	82.9.18.2	M	55°45'12.50"N
NHM	Abrantos, south of Tagus, Portugal	*C. lupus*	1937.2.10.2	M	39°17'6.20"N
NHM	Bosnia, Yugoslavia	*C. lupus*	1935.8.5.1	M	43°57'54.95"N
NRM	Ljusdal, Ramsjo	*C. lupus*	A580255	M	61°49'51.02"N
NRM	Jokkmokk	*C. lupus*	A583532	M	66°36'25.05"N
NRM	Orebro	*C. lupus*	A583547	M	59°16'30.95"N
NRM	Luktjomtjuolta, Vilhelmina	*C. lupus*	A590009	M	64°37'28.22"N
NRM	Lina alv station	*C. lupus*	A775097	M	67°14'52.40"N
NRM	Atran, Ogardet	*C. lupus*	A845131	M	57° 7'22.70"N
NRM	Hede, Norrstadjan	*C. lupus*	A895039	M	62°25'5.97"N
NRM	Kiruna-Gallivare, Gaddmyr	*C. lupus*	A925106	M	67°58'13.70"N
NRM	Boras	*C. lupus*	A965002	M	57°43'17.35"N
NRM	Jarna, Flaten, Dalarna	*C. lupus*	A995016	M	59° 7'20.40"N
NRM	Varmland, Eksharad, Halgan; Kolarkojan	*C. lupus*	995230	M	60°10'22.05"N
NRM	Jumkil kyrka, Uppsala	*C. lupus*	20005365	M	59°57'3.40"N
NRM	Uddalen, Ed, Dalsland	*C. lupus*	20035114	M	58°42'12.07"N
NRM	Ostermoren, Smedjebacken, Dalarna	*C. lupus*	20045305	M	60° 8'35.49"N
NRM	Dala Floda, Borlange, Dalarna	*C. lupus*	20035024	M	60°29'31.38"N
NRM	IV 225, Osmo, Sodermanland	*C. lupus*	20065027	M	58°59'4.38"N
NRM	Lanasberget, Grundsjo, Ljungaverk, Medelpad	*C. lupus*	20055287	M	64°49'1.71"N
NRM	Mullhyttan, Orebro, Narke	*C. lupus*	20065414	M	59° 9'11.95"N
NRM	Avik, Laxa, Narke	*C. lupus*	20075186	M	58°40'15.55"N
NRM	Malung-Appelbo, Dalarna	*C. lupus*	20085027	M	59° 7'60.00"N
NRM	Torsby, Ostmark, Sojensoasen, Dalarna,	*C. lupus*	20075373	M	60°16'36.44"N

NRM	Stormosse, Piro, Bjorneborg, Kristinehamn, Varmland	*C. lupus*	20085036	M	59°18'36.24"N
NHM	France	*C. lupus*	1843.12.29.7	F	46°44'12.10"N
NHM	Pyrenees	*C. lupus*	44.1.18.1	F	42°55'38.58"N
NHM	Nr Abrantos, South of the Tagus, Portugal	*C. lupus*	1938.12.7.1	F	39°17'5.82"N
NHM	Riocalado, Burgos, Spain	*C. lupus*	11.10.5.2	F	42°20'38.37"N
NHM	Kocane, Serbia	*C. lupus*	47.1121.a	F	43°11'4.00"N
NRM	Kiruna	*C. lupus*	A581198	F	67°51'20.88"N
NRM	South Finnskoga, Skrackarberget	*C. lupus*	A865126	F	60°40'60.00"N
NRM	Jadraas, 5km North	*C. lupus*	A915068	F	60°50'41.06"N
NRM	Vastra Amtervik, Hensgard	*C. lupus*	A935024	F	59°45'0.00"N
NRM	Nas-snoan, v71/jvg, Dalarna	*C. lupus*	A935178	F	61° 5'30.12"N
NRM	Nyskoga, Kringsberg, Bontjarn	*C. lupus*	A945045	F	60° 8'27.27"N
NRM	Vastmandland, Grythyttan	*C. lupus*	20005111	F	59°42'16.93"N
NRM	Narke, Degerfors, Atorp	*C. lupus*	20025005	F	59°14'20.77"N
NRM	Atorp 3.5 km NW, Degerfors, Varmland	*C. lupus*	20035026	F	59°15'48.67"N
NRM	Odlingen, Sillerud, Arjang, Varmland	*C. lupus*	20045040	F	59°19'0.00"N
NRM	Ovre Hurr, Tocksfors, Varmland	*C. lupus*	20065236	F	59°30'31.66"N
NRM	Rickebo, Hallbo, Bollnas, Halsingland	*C. lupus*	20065047	F	61°13'13.30"N
NRM	Ronnas, Ostra, Leksand, Dalarna	*C. lupus*	20075381	F	60°42'0.01"N
NRM	Jarbo, Backefors, Dalsland	*C. lupus*	20075314	F	58°43'59.56"N
NRM	Varmland, Nordmark, Algsjion 2 km S	*C. lupus*	20095063	F	58°50'3.72"N
NRM	Halsingland, Bollnas, Lottefors; Rv 83	*C. lupus*	20075312	F	61°25'13.48"N
NRM	Vastmanland, Hallefors, Ornviken, Holmtjarnstorp	*C. lupus*	20105028	F	59°42'59.97"N

Table 4.3. Localities and latitudes of modern European *C. lupus* specimens.

The localities of the modern wolf samples are illustrated in Figure 4.5.

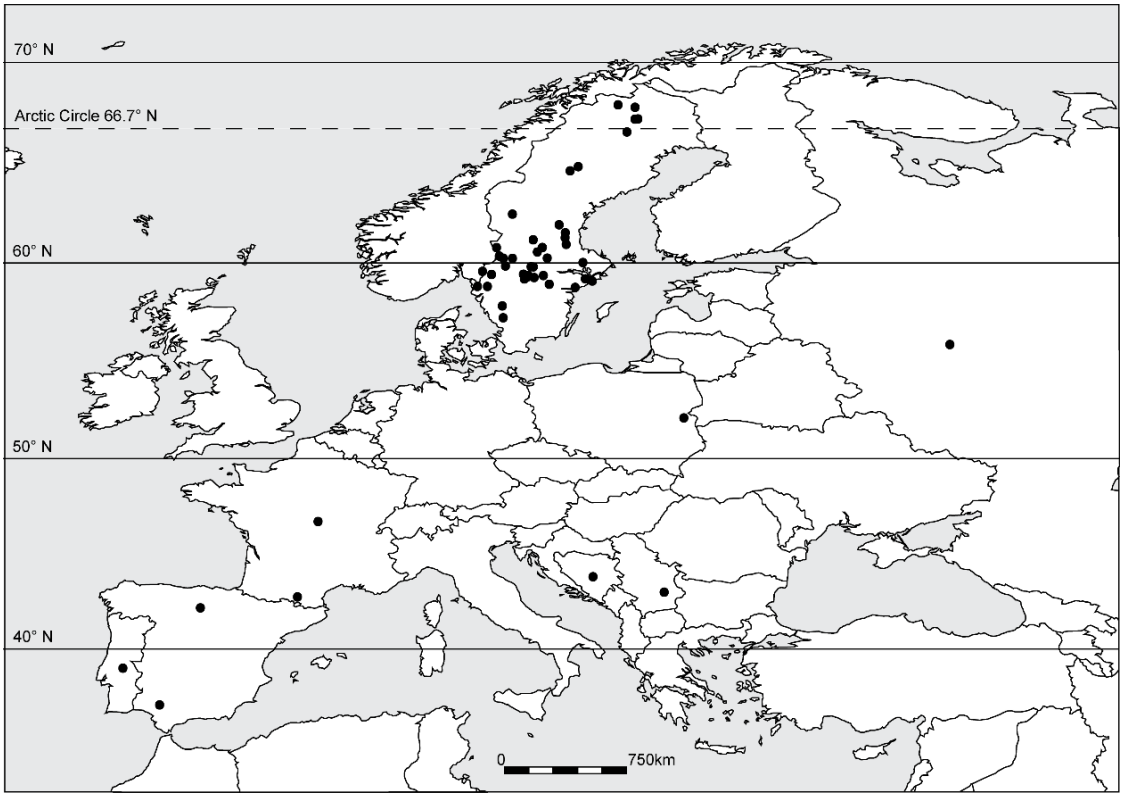


Figure 4.5. Map of western Europe indicating the localities of the modern *C. lupus* specimens used in the analyses. Latitude illustrated on map.

Other modern canids such as *Canis adustus, Canis aureus, Canis mesomelas, Canis simensis, Cuon alpinus* and *Lycaon pictus*, as well as subspecies of *C. lupus* such as *Canis lupus lupaster* and *Canis lupus arabs* were recorded from the NHM and Harrison Institute, Sevenoaks, Kent, for use in both body mass and dietary analyses of the Pleistocene canids.

As mentioned previously, the numbers of individuals recorded for these species are as follows: modern European *C. lupus*: 52, *C. l. arabs*: 10, *C. l. lupaster*: 6, *C. adustus*: 26, *C. aureus*: 31, *C. mesomelas*: 30*, Cuon alpinus*: 30, and *L. pictus*: 27.

4.2. Issues encountered in the analyses

A common problem in palaeontological research is the presence of incomplete material. Whole specimens are very rare and taking a complete suite of morphological measurements on a single individual is often not possible. Although a large amount of morphological measurements were taken during this research, only measurements representing a consistently large number of individuals were analysed (minimum 3). Furthermore, to avoid accidental repeated analysis of the same individual, either exclusively right or left orientations of parts were used in the analysis.

Another potential problem is low specimen numbers at any given site, which often results in small samples for a particular age grouping. For example, MIS 5c in the early part of the last cold stage is poorly known in Britain and is represented by only two sites (see Currant and Jacobi, 2001): Bacon Hole and Minchin Cave, both containing only one individual. Age groups with low numbers of individuals therefore had to be excluded on the grounds of potential unreliability, as well as unequal sample size in comparison to other age groups with more abundant remains.

The sites from Britain included here are either well dated through geochronology or correlated through biostratigraphy or lithostratigraphy with a particular climatic stage or sub-stage. However, for many of the mainland European sites, age estimates were often not as well constrained as for the British material, requiring broad age groups to be established to aid temporal analysis and correlation with British material. For the purposes of the analyses, these continental European age groups were assigned purely nominal numerical values as follows: 4=Early Pleistocene, 3=Middle Pleistocene, 2=Late Pleistocene and 1=Holocene. Each group was further divided into early, middle and late, with the decimal .8, .4, and .0 indicating these subdivisions. Thus, 2.8=early Late Pleistocene, 2.4=middle Late Pleistocene and 2.0=late Late Pleistocene. The temporal range of these age groups is shown in Figure 4.6.

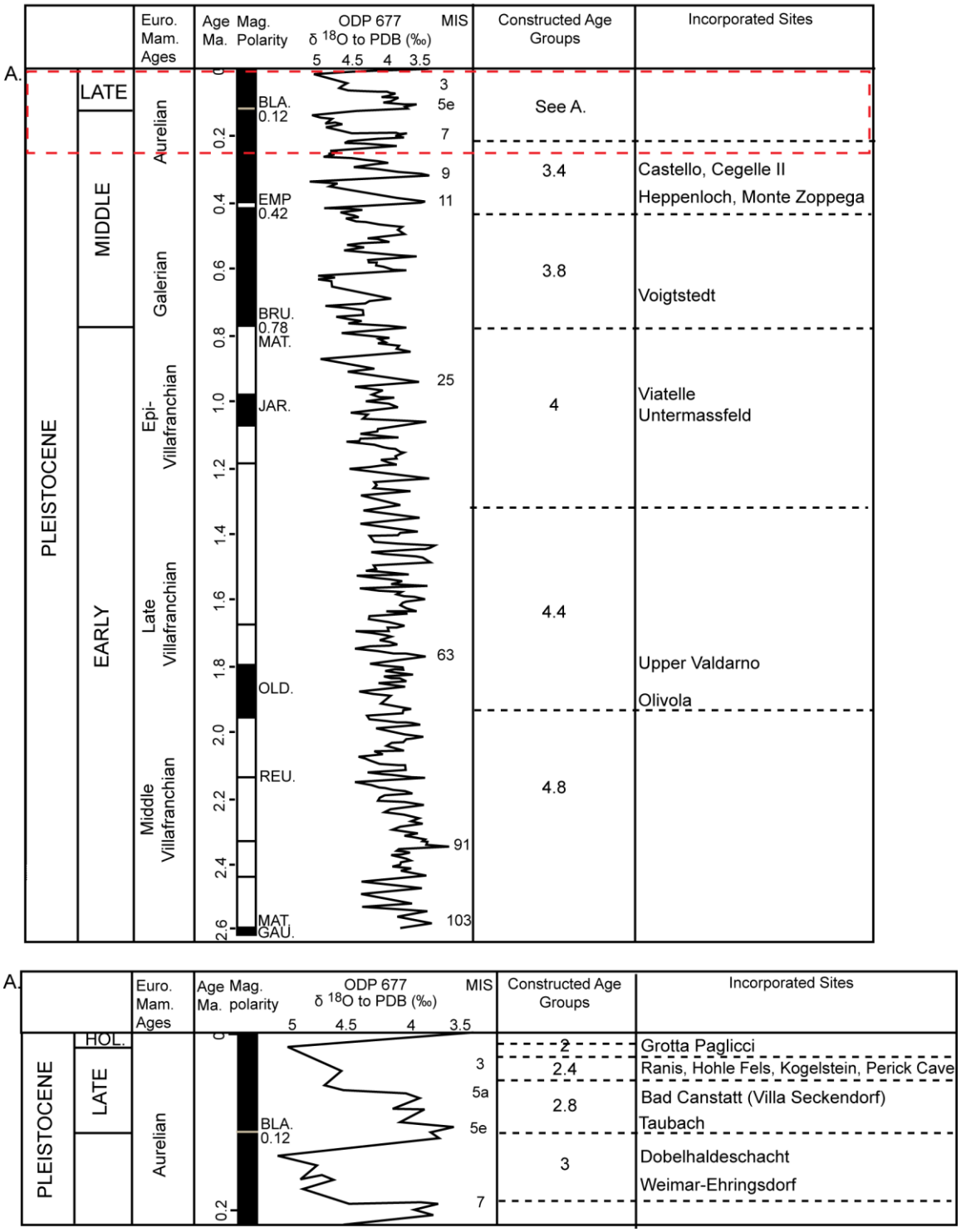


Figure 4.6. Chronostratigraphy of the constructed European age groups used in the analysis of mainland European material. Sites incorporated into each constructed age group shown. MIS ages shown illustrating equivalence with the age groups.

4.3. Measurements and preliminary analysis of distribution, correlation and variation

4.3.1. Cranio-dental measurements

Measurements of all available material were taken using both digital (for specimens <150mm) and non-digital callipers (for specimens with dimensions >150 mm) in millimetres (mm). Repeated measurements were taken weekly on a subset of material to ensure consistency. To increase comparability with previous studies of canids, measurements were derived from the literature, including Von den Driesch (1976) for the majority of dental, cranial and postcranial metrics, and supplemented by Van Valkenburgh and Koepfli (1993) and Van Valkenburgh et al. (2004) for certain dental and mandibular measurements. The measurements used in the analyses are shown in Table 4.4, and illustrated in Figure 4.7.

Measurement	Description
p4L	Maximum antero-posterior length of lower fourth premolar [a]
p4W	Maximum medio-lateral breadth of lower fourth premolar [a]
m1L	Maximum antero-posterior length of lower carnassial
m1Ltrig	Maximum antero-posterior length of the lower carnassial trigonid (paraconid and protoconid) [b]
m1Ltal	Maximum antero-posterior length of the lower carnassial talonid basin
m1W	Maximum medio-lateral breadth lower carnassial [a]
m2L	Maximum antero-posterior length of second lower molar [a]
m2W	Maximum medio-lateral breadth of second lower molar [a]
p1p4L	Length of the premolar row p1-p4 measured along the alveoli [a]
p2p4L	Length of the premolar row p2-p4 measured along the alveoli [a]
p1m3L	Length of the cheek tooth row p1-m3 measured along the alveoli [a]
p2m3L	Length of the cheektooth row p2-m3 measured along the alveoli [a]
p3p4B	Dentary breadth at the p3-p4 junction of the mandible [c]
p3p4D	Dentary depth at the p3-p4 junction of the mandible [c]
m1m2D	Dentary depth at the m1-m2 junction of the mandible [a]
m1m2B	Dentary breadth at the m1-m2 junction of the mandible [c]
P3L	Maximum antero-posterior length of upper third premolar
P4L	Maximum antero-posterior length of upper carnassial [a]
P4W	Maximum medio-lateral breadth of upper carnassial, including the protocone [a]
M1L	Maximum antero-posterior buccal length of first upper molar [a]
M1W	Maximum antero-posterior width of first upper molar [a]
M2W	Maximum medio-lateral breadth of the second upper molar
P1P4L	Length of the upper premolar row on buccal side[a]
C1M2L	Length from the oral upper canine to aboral border of the second molar [a]
P1M2L	Length of the upper cheek tooth row on buccal side [a]
M1M2L	Length of the upper molar row on the buccal side [a]

Table 4.4. Cranio-dental measurements used in the analyses. [a] Von den Driesch (1976), [b] Van Valkenburgh et al. (2004), [c] Van Valkenburgh and Koepfli (1993). Measurements illustrated in Figure 4.7.

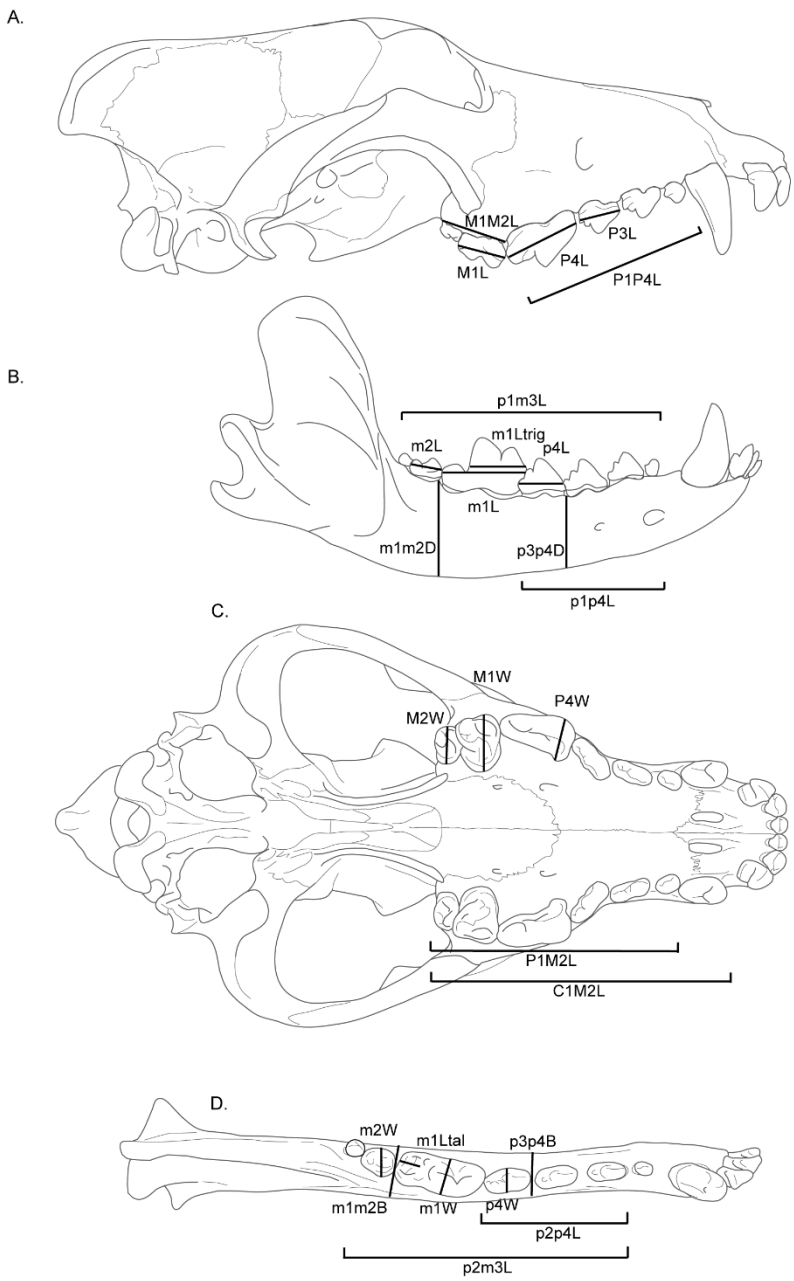


Figure. 4.7. Cranio-dental measurements used in the analyses illustrated on the skull and mandible of *C. lupus*. **A**: Lateral view of skull, **B**: Lateral view of mandible, **C**. Ventral view of skull focussing on palate and dentition, **D**. Dorsal view of right mandible focussing on dentition. Abbreviations of measurements in Table 4.4.

4.3.2. Relationship between the carnassials and body size

As introduced in Chapter 2, cranio-dental measurements have important correlations with diet. In addition, both the lower and upper carnassials (m1, P4) were used to estimate body

mass in the extinct canids. The m1 in particular is a well-used predictor of body mass (Legendre and Roth, 1988; Van Valkenburgh, 1990), based on its low variability, its well-developed and functionally-important role in canids and its correlation with body size (Legendre and Roth, 1988), indicating that it should scale predictably with body mass (Van Valkenburgh, 1990). This tooth is also frequently well preserved and abundant in the fossil record and has therefore been the focus for predictions of body mass in the current study, in order to maximise the number of individuals contributing to the body mass estimation.

4.3.3. MNI and NISP

The minimum number of individuals (MNI) was calculated using the most common dental, cranial or post-cranial element present in a site assemblage, or for individual strata if applicable. The number of identifiable specimens (NISP) was also calculated for all assemblages by counting the number of identifiable specimens of a species (e.g. *C. lupus*) at a site and by strata where applicable.

4.3.4. Distribution and outliers

Prior to more in-depth statistical analysis, the presence of outliers and the distribution of each measurement were assessed, in order to determine which type of statistical methods were appropriate to use, for example, either parametric or non-parametric methods (Sokal and Rohlf, 1995). For the detection of outliers, as well as an approximate assessment of distribution, graphical methods such as histograms and Quantile-Quantile plots (Q-Q plots) were used for visually assessing the data, followed by more formal normality testing using Shapiro-Wilk tests. These tests were all performed using SPSS version 19, and this programme was used in all further statistical analyses carried out.

Upon visual inspection of histograms, outliers in the data were identified by their plotting more than 2σ from the sample mean. Once identified, the outlier was removed from all further analyses. In total 31 outliers were removed from the measurement data. For *C. lupus*, removals included a p4 and P3L from Banwell, an m2W Stump Cross Cave, a P4L from Pin Hole Cave, and an M1 from Bosco's Den. Two outlying measurements for M2W were also identified in a modern wolf from northern Sweden and from Portugal. In some cases multiple measurements from the same individual were outliers, such as in Bosco's

Den (p1p4L and p2p4L), as well as Crayford (p1p4L, p2p4L, p1m3L, p2m3L, p3p4D, m1m2D).

For *C. mosbachensis*, an m2 from Untermassfeld and a P4L from Westbury were removed. For *C. arnensis*, single measurements of m1W, p4W, m2W, P4L, p3p4B and M1M2L were removed from Upper Valdarno specimens. Also from the Upper Valdarno, single measurements from *C. etruscus* of m1W, m1Ltal, m2W, p3p4D and p3p4B were removed, as well as two outliers of m1m2B. A single outlying measurement of m1m2B from *C. etruscus* of Olivola was also removed.

Although normal distribution was not assumed here, due to the frequently low number of individuals available for some measurements, it is acknowledged that an apparently non-normal distribution might result from low number of individuals, rather than a truly non-normally distributed population. The Shapiro-Wilk test is an evaluation method for testing the supposed normality of a complete sample (Shapiro and Wilk, 1965; Razali and Wah, 2011). The test is both scale- and origin-invariant, it is sensitive to outliers, and most importantly, it is also effective with small sample sizes (n< 20-50) (Shapiro and Wilk, 1965).

The Shapiro-Wilk test evaluates the null hypothesis (H_0), that a sample (X_1…, X_n) came from a normally distributed population. Based on the *p* value (the calculated probability) being more or less than the critical significance level (α), the H_0 is either rejected (e.g. if α=0.05, p<0.05) or retained (e.g. if α=0.05, p>0.05). The rejection of H_0 indicates that the sample is not from a normal distribution. By upholding H_0, the population is described as normally distributed. However, this does not confirm that the sample is normal, rather that it is *not* non-normal.

Each measurement used in the analysis was therefore assessed for outliers using histograms, with all identified outliers consistently removed from further analysis. Formal normality testing using Shapiro-Wilk tests was then carried out for each measurement. Measurements were grouped by species, for example the Pleistocene species *C. etruscus*, *C. arnensis*, *C. mosbachensis* and *C. lupus*, as well as by modern species used in multivariate analysis, namely golden jackal (*Canis aureus*), side-striped jackal (*Canis adustus*), black-backed jackal (*Canis mesomelas*), Asiatic dhole (*Cuon alpinus*) and wild dog (*Lycaon pictus*).

4.3.5. Linear correlations

After the removal of outliers and where the distribution was found to be normal, the presence of linear correlations between the measurements was explored using the parametric test of Pearson product-moment correlation. Determining how two variables co-vary is important, since establishing relationships between cranio-dental measurements is useful in understanding morphological relationships. Pearson correlation does not require the identification of either independent or dependent variables, and thus treats all variables as equal. The test does not require prior knowledge as to what kind of variable the data represent.

The calculated Pearson correlation coefficient (Pearson's r) indicates the strength of the correlation, with an r coefficient of 0.9 or -0.9 (for example) indicating a strong positive or negative correlation respectively. An r coefficient of 0.3 would indicate a weak correlation, with 0 indicating no correlation (Hawkins, 2009). The significance of the relationship between the two measurements is also calculated. The *p* value indicates either significance or non-significance by being more or less than the critical significance level (α), which is α=0.05.

4.3.6. Coefficient of variation

Variation was further explored in the analysed measurements by calculating the coefficient of variation (CV), as used by Gingerich and Winkler (1979) and Pengilly (1984) in a study of red and arctic foxes (*Vulpes vulpes* and *Alopex* (*Vulpes*) *lagopus*), as well as by Dayan et al. (2002) for Israeli canids. The CV is a measure of relative variation and is calculated as the sample standard deviation (SD), divided by the sample mean ($\bar{x}$) and multiplied by 100.

The CV was calculated for each species used in the analysis in order to explore which measurements had the lowest variability. This technique is particularly helpful in body mass estimation, where the least variable measurements are the most useful and thus more able to predict variation in body size rather than intraspecific variation.

4.3.7. Graphical comparisons of data

Graphical comparisons of all the analysed measurements were made, in order to visually explore and compare the data. Graphs illustrating the data for each measurement were created, showing both individual data, plotted by age group and identified by site, as well

as the mean and standard deviations of different age groups. Sites in Britain were compared with those from sites in mainland Europe, for both individuals and for data grouped by age group. Comparisons with published material from sites not included in this research were also made for *C. mosbachensis* from Petralona Cave, Greece, and L'Escale, France, from Kurtén and Poulianos (1977).

4.4. Analysis of allometric scaling and body mass

4.4.1. The modern canid dataset

In order to predict the body mass of the extinct Pleistocene canids (*C. etruscus, C. arnensis* and *C. mosbachensis*), a dataset of modern canids was used to create a predictive regression model (see Section 4.4.5). As the extinct canids all belong to the genus *Canis*, only members of the Family Canidae were used, rather than a much broader dataset with a range of different carnivores. This is because in carnivores, regressions based on Family affiliation were found by Van Valkenburgh (1990) to be better predictors of body mass than those based on multiple Families, likely due to scaling differences between them (see Section 4.4.4 for a discussion of scaling).

Although the restriction to the Canidae inevitably reduced sample size, a large range of different taxa was included to encompass the breadth of ecological, morphological and size variation seen in the canids, thereby providing as broad a basis as possible for body mass prediction and minimising any effects of phylogeny (Mendoza *et al.*, 2006). Subspecies were not included in the dataset to avoid it becoming taxonomically homogenous (effectively becoming a single sample) and artificially increasing its importance in the model (Mendoza *et al.*, 2006). Hence, subspecies such as *Canis lupus arabs* and *Canis lupus pallipes* were excluded from the analysis.

In total, 28 canid species were used, including side-striped jackal *C. adustus*, golden jackal *C. aureus,* black-backed jackal *C. mesomelas*, coyote *Canis latrans*, grey wolf *C. lupus*, Ethiopian wolf *Canis simensis,* maned wolf *Chrysocyon brachyurus,* Asiatic dhole *C. alpinus,* wild dog *L. pictus,* bush dog *Speothos venaticus,* arctic fox *Alopex lagopus,* crab-eating fox *Cerdocyon thous*, culpeo *Pseudalopex culpaeus*, South American grey fox *Pseudalopex griseus*, pampas fox *Pseudalopex gymnocercus,* sechura fox *Pseudalopex sechurae,* hoary fox *Pseudalopex vetulus,* grey fox *Urocyon cinereoargenteus,* island fox *Urocyon littoralis,* Bengal fox *Vulpes bengalensis,* cape fox *Vulpes chama*, kit fox *Vulpes macrotis,* pale fox

Vulpes pallida, Rüppell's fox *Vulpes rueppellii,* red fox *Vulpes vulpes,* raccoon dog *Nyctereutes procyonoides* and bat-eared fox *Otocyon megalotis*.

The body weight of modern canids was taken from multiple published sources including: Asa and Cossios (2004), Asa et al. (2004), Atkinson and Loveridge (2004), Ballard et al. (2000), Bekoff (1977), Bueler (1973), Caro and Stoner (2003), Cavallini (1995), Chesemore (1975), Cohen (1978), Cuzin and Lenain (2004), Dalponte and Courtneay (2004), de Mello Beisiegel and Zuercher (2005), Dietz (1985), Fritzell and Haroldson (1982), Fuller and Cypher (2004), Geffen et al. (1996), Gittleman (1986), Gonzalez del Solar and Rau (2004), Haltenoth and Roth (1968), Hattingh (1956), Jhala and Moehlman (2004), Jimenez and Novaro (2004), Johnsingh and Jhala (2004), Kingdon (1977), List and Cypher (2004), Loveridge and Nel (2004), Lucherini et al. (2004), Macdonald (2009), Mech (1974), Nel and Maas (2004), Nowak (1999), Prestrud and Nilssen (1995), Roemer et al. (2004), Sillero-Zubiri (2004), Sillero-Zubiri and Gottelli (1994), Stuart and Stuart (2004), Ward and Wurster-Hill (1990) and Woodroffe et al. (2004). Modern *C. lupus* body weight was also included from the records of the Naturhistoriska riksmuseet.

Where body mass ranges of a species or sex were published, the median was taken. Otherwise, where only mean weights were published, the mean was calculated from the combined available sources. Where possible, separate male and female weights were taken, although this was not available for all species and in those cases, the amalgamated body weight for both sexes was used.

A caveat is that body mass predictions are limited to animals within the extant size range of the dataset, since extrapolation beyond the size of the modern animals is theoretically questionable (Andersson, 2004a). However, the extinct canids are considered to be smaller than modern wolf and therefore, their estimated body weights were not expected to exceed the modern dataset. It nevertheless remains a possibility that the predictions of Pleistocene *C. lupus* body mass may exceed mean values for modern *C. lupus*.

The number of specimens of each species used in the modern canid dataset ranged from four to ten individuals, varying between one and seven when split into males and females. Wherever possible, samples were of similar size to minimise risk of over representation of one species over another (Mendoza *et al.*, 2006), and equal numbers of male and females within a species were used. All individuals were wild-caught adults, in order to eliminate problems associated with morphology in captive animals (O'Regan and Kitchener, 2005).

For the modern material, cranio-dental measurements were taken by the author for *C. adustus*, *C. aureus, C. mesomelas, C. simensis, C. lupus, C. l. arabs, C. l. pallipes*, *C. alpinus, L. pictus* and *Vulpes vulpes* from the following institutions: Department of Zoology, Natural History Museum, London, Naturhistoriska riksmuseet, Stockholm, University Museum of Zoology, Cambridge, the Harrison Institute, Sevenoaks and Royal Holloway University of London. For the remaining species, measurements were taken from Palmqvist et al. (2002).

4.4.2. Transformation of data

Transformation of variables will result in data being more amenable to statistical analysis (Zar, 2010). In particular, transformation of data often improves linear regression (Sokal and Rohlf, 1995), and is commonly carried out to facilitate body mass prediction analysis (e.g. Legendre and Roth, 1988; Van Valkenburgh, 1990; Andersson, 2004a).

The aim of transforming both X and Y axis variables for regression is to achieve a normal and homoscedastic distribution of data around the regression line (Sokal and Rohlf, 1995). Thus, the closer the 'fit' of the data to the regression line, the more instructive that line is in explaining the variation within the dataset. The process is also often used when the range of data covers several orders of magnitude.

Although the data used in this research were checked for both outliers and normality, the body mass and predictor measurement data were transformed into base 10 logarithms (Log_{10}), following common body mass predicting protocol (e.g. Van Valkenburgh, 1990; Andersson, 2004a), in order to create the best possible model for making estimates. In particular, when assessing allometric scaling relationships, it is considered easier to evaluate logarithmically-transformed data (Smith, 1993).

However, the remaining measurements not used in regression analyses were not transformed, and thus were analysed in their original arithmetic form. Although transformation can induce normality by making the data homoscedastic (Sokal and Rohlf, 1995), this was not considered an issue here as the data had already been proved to be normally distributed, they had been checked for unequal variances (heteroscedasticity) where appropriate, and they were not found to range over several orders of magnitude. Transformation is hence not always necessary and should be used judiciously.

The results from logarithmically-transformed data also require careful interpretation, as when using regression to predict values, the mean estimates derived are often biased due to subsequent detransformation. This will be further discussed in section 4.4.5.4.

4.4.3. The use of regression

In its simplest form, regression analysis investigates and models the relationship between variables. In linear regression, the relationship is modelled between two variables: the independent (also known as the predictor or the regressor) variable on the X axis, and the dependent (i.e. the response) variable on the Y axis. The objective is to estimate the unknown Y, as a function of X.

The assumptions of regression outlined by Zar (2010) are: 1) that the data represent a random sample of the population, 2) that they are normally distributed, 3) that they have homogeneous variance, 4) that there is a linear relationship between the X and Y axis variables, and 5), that the X axis variable is obtained without error. However, with regards to 5), the assumption that errors on the X axis variable are negligible, or at least small in comparison to the errors related to the Y axis variable, is also allowed (Zar, 2010). As introduced previously, logarithmic transformation of data can fulfil the majority of these criteria.

Least squares regression is commonly used to model the association between body mass and various dental, cranial and skeletal predictor measurements (Legendre and Roth, 1988; Van Valkenburgh, 1990; Ruff, 2003; Andersson, 2004a), especially when there are uncertainties (i.e. errors) in the *y axis dependent* variable. For example, Legendre and Roth (1988) preferentially chose least squares regression to minimise the associated dependent variable error in their estimation of body mass.

However, it is quite possible that both variables contain a certain degree of error, beyond the control of the researcher, as indicated by Zar (2010). Thus, an alternative to using a model I regression method such as least squares (as described above), which only assumes measurement error in the dependent variable, is a model II method such as reduced major axis regression, which assumes that both variables contain error (Sokal and Rohlf, 1995). The choice of regression method for prediction has been much debated and no method may be correct for all purposes (see Smith, 1994).

Smith (1994) also proposed that measurement error may not be as important as previously thought, since measurement error is 'based on the random imprecision and inaccuracy of measurements taken in the physical sciences, not on the meaningful deviations from a perfect bivariate relationship that would remain with biological traits no matter how well measurements were taken' (Smith, 1994 p. 242). Thus the least squares method, when used appropriately, was therefore considered by Smith (1994) as an important and appropriate procedure.

Least squares regression was therefore used for both the analysis of scaling relationships and for body mass estimation. Carnassial length was accordingly first regressed on body mass to explore the allometric scaling relationships between the variables (X axis variable is body mass, Y axis variable is carnassial length). Following this, body mass was then regressed on carnassial length to create the predictive model (X axis variable is carnassial length, Y axis variable is body mass).

Since both X and Y variables are therefore used interchangeably, both are considered as containing measurement error to some extent, beyond the control of the author. Thus, following Anderson (2004a), variable dependency was assumed as present, and that as the main aim here was to explore both the scaling relationship followed by the creation of a predictive model, the two variables were considered as simply a dependent one regressed on an independent one, with the latter assumed to not contain error.

Linear regression was chosen over multiple regression on the basis that it would be more applicable to a larger number of individuals, due to the incomplete nature of the fossil record.

4.4.3.1. Validating the regression model

Departure of points from the regression line can help establish the overall goodness of fit of the regression (Sokal and Rohlf, 1995). However, to check the accuracy of the regression model more thoroughly, the residuals need to be examined for outliers, leverage and influence.

The residuals represent the difference between the observed values of the dependent variable and the predicted values from the regression model. The residuals were checked for regressions investigating both allometric scaling and body mass estimation.

Potential outliers were examined initially by plotting the studentised residual against the X axis variable (log_{10} body mass in allometric scaling regressions, log_{10} carnassial length in body mass estimation). The scatter of points should be evenly distributed above and below 0 on the Y axis (i.e. homoscedastic) (Zar, 2010). Residual outliers are identified by having a residual value >2.0, and can affect the scatter of points. Two types of outliers are possible, relating to either the Y axis dependent variable or to the X axis independent variable.

The residuals were further examined for their leverage and influence as it is possible for non-outliers, as well as outliers, to have varying degrees of leverage and influence over the model. It is therefore important to identify the proportion of leverage and influence. For example, a high leverage residual can control the fit of the regression line, but if not identified as an outlier, it may not be detrimental. However, if an outlier has both high leverage and influence, it should be removed from the model.

Leverage was determined by the hat matrix diagonal, with high leverage determined by: $h_i > 2p/n$, where p= number of predictors, n= number of observations (Seber and Lee, 2003). Hence, residuals with leverage greater than the hat matrix diagonal may be controlling the regression line.

Influence was determined by Cook's D (Cook, 1977), with high influence determined by: $D_i > 4/n$, where n= number of observations (Bollen and Jackman, 1990). Hence, residuals with influence greater than Cook's D may also be influencing the model.

The residuals were also checked for normality using Shapiro-Wilk tests and Q-Q plots. If residuals were found as outliers during earlier examination, as well as by the normality tests and Q-Q plots, in addition to having high leverage and influence, they were removed from the model and the remaining data re-analysed.

4.4.4. Scaling of carnassial length with body mass

Carnassial length was regressed on to body mass using least squares regression to investigate the scaling of the predictor variable. Allometry refers to the scaling relationship between the size of a characteristic and the size of the body as a whole. If the scaling between a certain characteristic and body size is similar, then they have geometric similarity and they are scaling with isometry. Deviations from geometric similarity can be either positively or negatively allometric, indicating that the characteristic is not scaling similarly.

Geometric similarity predicts that linear measurements (*l*) scale to body mass (*M*) as: $l \propto M^{0.333}$ (Andersson, 2004a), or simply, that the isometric slope of log length (length^1), plotted against log body weight (proportional to length^3), is 0.33.

Thus, a variable that scales with geometric similarity to body mass has an expected slope of 0.33. The deviations from this slope therefore indicate either positive or negative allometry.

Following Huxley (1932), simple allometry can be explained by the following exponential relationship:

$$Y = aX^b$$

Where Y = measurement variable, X = body size, a = constant, b = allometric coefficient

When the variables are logarithmically transformed (Log_{10}), both sides of the equation are subsequently transformed into logarithms, creating the following linear equation:

$$\text{Log Y} = \log a + b \log \text{X}$$

Where a = y axis intercept, b = the allometric coefficient

By investigating how variables scale in extant members of the canid family, it is reasonable to assume that scaling will be similar for the extinct members of that family. Hence, prior to estimating body mass in the fossil canids, the predictor measurements (m1L, P4L) were regressed on body mass to evaluate the scaling of these measurements.

Having determined the allometric coefficient for carnassial length, the rate at which it scales with body size can be identified, in terms of whether it indicates an equal response from both carnassial length and body size (isometry), or alternatively that as body size increases, carnassial length increases at a slower rate (negative allometry) or finally that as body size increases, carnassial length increases at a faster rate (positive allometry). This therefore affects body mass estimations since the tooth may be over- or under-estimating body size.

4.4.4.1. Least squares regression of carnassial length on body mass

Using the 28 species in the extant canid dataset, least squares regression was used to model the scaling relationship between carnassial length (either m1 or P4) and body mass. As discussed, both variables were log_{10} transformed prior to analysis.

The coefficient of determination (r_2), standard error (SEE), standard error of slope (SE_b), and associated *t* test *t* value and *p* value for the slope (*b*), were identified for each regression. The significance of the regression was tested using ANOVA, and the significance of the slope was tested by *t* test.

The correlation between the independent and dependent variable was tested by Pearson product moment correlation. Residuals were then examined for outliers, leverage and influence (see 4.4.3.1). If removal of residuals was required, the modified extant canid dataset was then re-analysed following the above protocol.

4.4.4.2. Significance of the allometric coefficient (*b*)

To test whether the allometric coefficient (*b*) for both regressions using m1L and P4L was significantly different from the expected slope of geometric similarity (*b* = 0.333), a *t* test was used with the null hypothesis (H_0) that H_0: $\beta = \beta_{0.333}$: that the slope representing the allometric coefficient (β) created by regression is equal to the slope of geometric similarity ($\beta_{0.333}$). Significance was tested using the following *t* test equation (Zar, 2010):

$$t = \frac{b - \beta_{0.333}}{SE_b}$$

Where *b* = allometric coefficient, $\beta_{0.333}$ = geometric similarity, SEb = standard error of slope.

The calculated value of *t* is then compared to the critical value of *t*, which is based on $t_{\alpha\,(1),\,d.f.)}$ where α = 0.05, d.f. = n-2.

If the calculated value of *t* is less than the critical value of *t* ($t \leq t_{\alpha\,(1),\,d.f.}$) the H_0 is kept, indicating no significant differences present between the slopes. If the value of *t* is greater than the critical value of t ($t \geq t_{\alpha\,(1),\,d.f.}$) then the H_0 is rejected and significant differences are present.

4.4.5. Body mass estimation

As discussed, least squares regression was used to model the relationship between body mass of selected extant canids and carnassial length (m1 or P4). The resultant regression equation can then be used to predict an estimate of body mass for the Pleistocene canids. The regression equation is as follows:

$$y = mx + c$$

Where y= y-axis variable, m=constant, x=X-axis variable, c= constant

Prior to regression, the mean values of body weight, m1L and P4L were $\log_{10}$ transformed to enable the best possible relationship between body mass and measurements to be created. Thus the regression equation becomes:

log body mass = m (log measure)+ c

Where m=slope, c =y-intercept

This equation is then used to estimate Pleistocene canid body mass by entering the fossil tooth measurement (in $\log_{10}$ form) into the equation.

4.4.5.1. Least squares regression of body mass on carnassial length

As with the analysis of allometric scaling, the extant canid dataset was used by least squares regression to model the relationship between body mass and carnassial length (either m1 or P4), in order to create a predictive model for estimating Pleistocene canid body mass. As discussed, both variables were $\log_{10}$ transformed prior to analysis.

The coefficient of determination (r^2), standard error (SEE), standard error of slope (SE_b), and associated *t* test *t* value and *p* value for the slope (*b*), were identified for each regression. The significance of the regression was tested using ANOVA, and the significance of the slope was tested by *t* test.

The correlation between the independent and dependent variable was also tested by Pearson product moment correlation. Residuals were then examined for outliers, leverage and influence (see 4.4.3.1.) and re-analysed as required.

4.4.5.2. Comparing body mass estimating regression equations

The slopes created by the least square regression and used in body mass estimation were tested for their significance using the null hypothesis (H_0) of H_0: $\beta_1 = \beta_2$: where the slope (β_1) from regression of body mass and m1L equals the slope (β_2) of body mass and P4L.

To test whether the slopes of the regressions were significantly different, a Student's *t* test was used using the following equation from Zar (2010):

$$t = \frac{b_1 - b_2}{Sb_1 - b_2}$$

Where t = t test statistic, b = slope, Sb = standard error of slope.

The calculated value of t using the key regression information is compared to the critical value of t, which is based on $t_{\alpha\,(2),\,d.f.)}$ where $\alpha = 0.05$, d.f. = n-2.

If the calculated value of t is less than the critical value of t ($t \leq t_{\alpha\,(2),\,d.f.}$), the H_0 is kept, indicating no significant differences present between the slopes. If the value of t is greater than the critical value of t ($t \geq t_{\alpha\,(2),\,d.f.}$), then the H_0 is rejected and significant differences are present.

4.4.5.3. Measurements of prediction accuracy

As well as the regression models being tested for their overall significance by ANOVA, and the significance of their slopes by *t* tests, predictive power of the regression equations was also assessed by comparing the coefficient of determination (r^2), the standard error (SEE), the percent prediction error (%PE) and the percent standard error of estimate (%SEE).

The coefficient of determination (r^2) indicates the correlation between the predictor variable and body mass, with high values representing high correlation, and thus better prediction.

The percentage standard error of the estimate (%SEE) is a measure of predictive precision, reflecting the overall ability of the independent variable in predicting the dependent variable. The %SEE was calculated as the antilog (10^) of (2+SEE)-100 (following Van Valkenburgh, 1990). Thus, a low %SEE indicates an equation with higher predictive accuracy.

The percentage prediction error (%PE) indicates the percentage difference between the actual body weight and the predicted body weight by the regression (Van Valkenburgh, 1990) and is therefore a measure of the accuracy of the equation in predicting body mass

The %PE of body mass for each equation was calculated as: ((actual BM – predicted BM)/predicted BM) x 100 (following Smith, 1984). The mean %PE of all the species used to create the predictive model then represents overall %PE for that regression, and thus enables comparisons of prediction accuracy. Ideally, the lower the %PE, the better the equation at predicting body mass.

4.4.5.4. Correcting for detransformation bias

Logarithmic transformations can potentially alter the structure of the data, making arithmetic and logarithmic versions of the same data not equivalent for statistical analysis (Smith, 1993). Transformation introduces bias into the data (Sprugel, 1983), and is evident as a result of detransforming $\log_{10}$ values back into arithmetic values.

Bias is defined as the difference between the mean of a sample of estimates and the true value of the parameter of interest (Smith, 1993). To counteract bias, upon detransformation back into arithmetic units, a correction factor was applied following Smith (1993) to the estimated body masses.

The Quasi-Maximum Likelihood Estimator (QMLE) is one of the most commonly-used bias correcting methods (Ruff, 2003). The residual mean square (RMS) is used, which is equal to the mean square error (S^2). This value is given in the SPSS output of the regression statistics.

The RMS must be adjusted to suit $\log_{10}$ transformed data (Sprugel, 1983), i.e. (RMS x 1.1513). Using this adjustment, QMLE is then calculated as (exp(adjusted RMS/2)). This correction factor is then multiplied with the detransformed predicted value, correcting the bias present. However, QMLE has a problem with overcompensating bias (Smith, 1993), which is why a secondary correction factor was also calculated for comparison.

The Ratio estimator (RE) is calculated as: (mean observed Y values/mean detransformed predicted Y values). The calculated correction factor is then applied to the predicted value, as with QMLE. However, like QMLE, potential over- and under-estimation of bias is possible, based on issues with linearity, normality or heteroscedasticity.

4.4.5.5. Calculating confidence intervals

As logarithmic transformation alters the structure of the original data, upon detransformation back to arithmetic units, measurements of error such as standard deviation have no value. In light of this, 95% confidence intervals were calculated for the body mass estimates whilst in $\log_{10}$ scale, and then detransformed into linear scale in order to quantify the reliability of the estimates (Sokal and Rohlf, 1995). 95% confidence intervals (CI) were calculated following Ruff (2003) and Zar (2010) for the body mass estimates as:

$$\pm SEE \times t_{(100\text{-}CI)(2),\ d.f.}$$

with degrees of freedom d.f. =n-2

As the CI are calculated in $\log_{10}$ units, once detransformed the correction factor must be applied by multiplication to the CI.

4.4.6. Sexual dimorphism and Bergmann's rule

For the modern *C. lupus* sample, sexual dimorphism was quantified between males and females. However, due to the incomplete nature of the palaeontological record, determination of sex for the Pleistocene material was often not possible. In light of this, the differences between modern known male and female wolves were examined, in an attempt to generate a broad estimate of potential dimorphism in the Pleistocene species.

The effect of Bergmann's Rule on the modern *C. lupus* dataset was also determined, using the latitude of an individual's provenance, and m1 length as a proxy for body size.

4.4.6.1. Sexual dimorphism in measurements

Following Dayan et al. (1992), the percentage of sexual dimorphism was calculated as the difference between the mean male and mean female measurements ([mean male – mean female] x 100). The differences between males and females were further investigated using independent sample *t*-tests, with variation examined using Levene's tests.

4.4.6.2. Relationship between Bergmann's Rule and sexual dimorphism

Latitude and m1L in modern *C. lupus* were used to investigate whether any change in m1L (used as a proxy for body size) occurred with increasing latitude. This was further developed by separating the modern sample into males and females, to see whether sexual dimorphism was evident in the latitudinal scope of the data. Pearson correlation and least squares regression were used to examine correlations between proxy body size and latitude for each sex.

To investigate the presence of sexual dimorphism during the Pleistocene, individuals from Banwell Bone Cave (MIS 5a) were used as a 'test case', and compared to the modern *C. lupus* males and females both graphically and by *t* tests. The potential males and females

identified from Banwell Bone Cave were also tested using *t* tests to examine how different the groups were, and thus how well the groups represented males and females.

4.5. Analysis of diet

4.5.1. Principal Components Analysis

Principal components analysis (PCA) was used as a preliminary investigatory tool, to investigate which measurements caused the highest variation in the dataset, as well as to visualise and explore the measurement data. Large sample sizes are required for a PCA, thus the species data were combined into a more substantial canid dataset.

Although checked separately (section 5.1), correlations between the measurements were assessed by the PCA using Pearson correlation, as the PCA works by converting a set of potentially correlated variables into a set of linearly uncorrelated variables called principal components. Highly correlated measurements were subsequently removed from the analysis as both very low and very high correlations can cause loading onto a single principal component. Their removal thus provides the simplest explanation of variation within the data. The determinant of correlation for the correlation matrix was used as an indication of any remaining linear dependencies if =>0.

The suitability of the data for carrying out a PCA was explored using the Kaiser Meyer Olkin measure (KMO) of sampling adequacy and the Bartlett's Test of Sphericity. The KMO indicates the proportion of variance present in the measurements that may be caused by underlying factors, such as correlation. In contrast, the Bartlett's Test of Sphericity tests the null hypothesis that the correlation matrix is an identity matrix (the simplest square matrix where the diagonal elements =1, and the remaining elements =0), and therefore that the measurements are unrelated and unsuitable for use with a PCA.

The PCA reduces the number of variables into principal components, whereby the most important components are identified by eigenvalues >1. Varimax orthogonal rotation was used to create the simplest structure in the dataset, in order to visualise which measurements were loading onto each principal component. The component loadings therefore represent the correlation between each measurement and the component.

The ability of the extracted principal components to explain the variation in the dataset can also be tested, to identify how well the components represent the data.

4.5.2. Analysis of variance: one-way ANOVA

One-way analysis of variance (ANOVA) was used for analysing the variance between more than two unrelated samples, by establishing whether it can be accounted for by sample error alone (Hawkins, 2009). To fulfil the criteria for using one-way ANOVA, the data need to be normally distributed, the analysed samples need to be independent, and the variances homogeneous (homoscedastic) (Sokal and Rohlf, 1995). As outlined in section 4.3.4, all data were checked for outliers and normal distribution. To check for the equality of variances, Levene's test was used. The null hypothesis (H_0) was: *there is no difference between the populations from which the samples come from*. The critical significance level (α) = 0.05 for all analyses.

One way ANOVA was specifically used to:

1) analyse variances between age groups of the same species, in order to investigate temporal difference through the Pleistocene.

2) analyse variance between species groups, in order to examine variation between the Pleistocene canid species.

If a measurement was found to be significant by ANOVA, subsequent *post hoc* tests were then used to make multiple comparisons between the age groups. It is statistically invalid to employ multiple *t* tests to compare means, as this increases the risk of committing a Type I error, that is to say the probability of incorrectly rejecting at least one H_0 (Zar, 2010).

Hence, for measurements with equal variances (as found by the Levene's test), Tukey Honestly Significant Difference (HSD) was used, whereas for measurements with unequal variances, Dunnett's T3 was used.

4.5.3. *t*-test

Where only two samples were present, *t* tests were used to analyse variance and assesses whether the variance between the two unrelated samples could be accounted for by sample error alone (Hawkins, 2009).

Like one-way ANOVA, data used in *t* tests need to be normally distributed and independent. The test assumes equality of the two sample variances (Sokal and Rohlf, 1995), and a Levene's test was used to check equality of variance. If found unequal, then an alternative result value given in the analysis based on variances *not* being assumed as equal

was used instead. The null hypothesis (H_0) was: *there is no difference between the populations from which the two unrelated samples come from*. The critical significance level (α) = 0.05 for all *t* tests.

t tests were used to:

1) analyse the variance between two temporal groups of the same species, where not enough groups were present to warrant to use of one-way ANOVA.

2) analyse the variance between two groupings separated by climatic affinity (cold- and warm-climate), representing the glacial and interglacial conditions of Pleistocene Britain.

3) analyse the variance between two regions, such as Britain and mainland Europe, using material of similar chronological age to determine any disparity.

4.5.4. Stepwise Discriminant Analysis

Standard Discriminant Function Analysis (DFA) is used to predict group membership from a set of predictor variables (Tabachnick and Fidell, 1996). The cranio-dental measurements represent the independent predictor variables, whereas either age groups or species groups represent the dependent variables. Thus, the measurements that are the best predictors of either age group or species group membership can be identified.

DFA works by creating one or more linear combinations of predictor variables in order to predict which group the cases (or measurement values) belong to. Thus, intercorrelations between the independent variables need to be low, in order to strengthen the predictive power of the model. In similarity to the PCA, correlations between the variables are assessed by the DFA.

Rather than allowing all predictor variables to enter the analysis at once, as in standard DFA, the stepwise DFA method instead uses set statistical criteria to determine order of entry into the analysis (Tabachnick and Fidell, 1996). The stepwise method therefore identifies and automatically selects the best set of predictor variables to use in discriminating between groups. This method is particularly useful when all predictor variables have the same priority in the analysis.

The selection method used here was Wilks' Lambda, which is a direct measure of the proportion of variance. The stepwise method then chooses the independent variables for entry into the model based on how much they lower the Wilks' Lambda, since smaller

values of Wilks' Lambda are indicative of greater discriminatory ability. At each 'step', the variable that minimises the overall Wilks' Lambda is thereby entered into the analysis.

This selection method is based on the F value, whereby the independent variable is entered into the model if its F value is greater than the default F entry value. The default F value was used here, with the F to enter = 3.84, and F to remove = 2.71. Hence, an independent variable is entered into the model if the independent variable F value > default entry F value, and removed if the independent variable F value < default removal F value.

The stepwise method, however, has some associated problems. For example, the order of entry of predictor variables into the analysis may be based on trivial differences in the relationships among the predictors that do not reflect real population differences (Tabachnick and Fidell, 1996). This bias can be reduced by using cross validation in the model.

The stepwise DFA was used to predict group membership of the temporal groups of *C. lupus* using British material from MIS 7, 5a and 3, as well as modern *C. lupus* from Sweden. The aim was to determine which measurements were the best at discriminating between the age groups, and thus indicate how diet varied temporally.

Based on the same principle, stepwise DFA was also used to predict group membership into the species groups of *C. etruscus, C. arnensis, C. mosbachensis* and *C. lupus*, again to highlight which measurements were the best at discriminating between the species, and to indicate how diet varied between the species.

Finally, stepwise DFA was used to examine the differences in diet between the Pleistocene canids and the modern canids, *C. adustus, C. aureus, C. mesomelas, C. alpinus* and *L. pictus*, in order to establish whether any of the Pleistocene canids had similar diets to modern species.

Prior to independent variable (e.g. measurement) selection, the predictive ability of the measurements was assessed using tests of equality of group means (Wilks' Lambda) and mean differences (ANOVA). Correlations between measurements were also examined by the model. Log determinants and Box's M were also employed to measure the variability between the groups (e.g. age, species).

The stepwise method then selects variables based on their ability to lower Wilks' Lambda, and the number of steps used is identified. From the number of steps, discriminant functions are created. The related eigenvalues, percentages of variance, cumulative

variance and canonical correlations are all identified for the discriminant functions, which are also tested for their discriminatory ability.

The correlation coefficient for each measurement to the discriminant functions is identified in the structure matrix, with group centroids (group means) also shown for each discriminant function.

The ability of the model-created discriminant functions in explaining the variation within the original dataset is also assessed, with the percentages of correctly and incorrectly classified cases into each dependent group (e.g. age or species) displayed. These results are based on both the original data (without correction for model bias) and on cross-validated data, which counteracts any bias present in the model. An overall percentage of discriminant ability (for both the original and cross-validated data) are also given, as a final indication of model strength.

4.5.4.1. Reducing the effect of size in the species stepwise DFA

As the Pleistocene species were identified from the outset as having different body sizes, Mosimann shape variables (Mosimann and James, 1979) were calculated for all the measurements to counteract the effect of size in the species group stepwise DFA. Various authors have employed these variables, such as Rosemann-Weaver (2004) for craniometric diversity in humans, and Meachen-Samuels and Van Valkenburgh (2009) for indicators of prey size choice from cranio-dental measurements in felids.

Mosimann shape variables are represented by the ratio of a variable to the geometric mean (Mosimann and James, 1979). The geometric mean is the N_{th} root of the product of N variables, and is equivalent to a linear dimension (Meachen-Samuels and Van Valkenburgh, 2009). The shape variables were therefore calculated as each original variable (i.e. measurement), divided by the calculated geometric mean of all the variables together. It should be borne in mind that these shape variables are ratios of data, and are therefore at risk of being affected by size dependency, which will be explored in the next section.

4.5.5. Morphometric ratios

In morphometric analysis, it is often common to use ratios of linear measurements to reflect aspects of diet (Van Valkenburgh, 1988a, 1989, 1991; Van Valkenburgh and Koepfli, 1993; Van Valkenburgh *et al.*, 2004), whereby functionally-significant measurements are

combined into morphometric ratios describing tooth shape rather than tooth size. These can be used to reflect the relative proportions of flesh, bone and non-flesh foods in the diet (Van Valkenburgh, 1988a, 1989).

However, the appropriateness of using morphometric ratios is much debated (e.g. Corrunccini 1975; Atchley *et al.*, 1976; Atchley, 1978). For example, Atchley et al. (1976) found ratios failed to remove the effect of size, and these authors concluded that ratios generally confuse and often invalidate analyses of the original raw data. Although acknowledging their relative simplicity and ease of use for analysis, Albrecht (1978) similarly considered that ratios are best avoided due to their apparent simplicity masking complex statistical and conceptual difficulties, which results in misleading conclusions. In spite of these problems, ratios have continued to be used, but with caution. Van Valkenburgh and Wayne (1994) considered their use of ratios justified as the ratios had been previously proven to be functionally indicative of diet, as well as only being used on three jackal species of similar body size, thereby removing the problem of difference in size. In contrast, due to the potential size issues involved, Andersson (2005) advocated direct analysis of linear measurements instead of ratios, thereby removing the ratio problem from all analyses.

4.5.5.1. Morphometric ratios: a test case

Because of potential complications resulting from size, analysis of diet was done here using linear data rather than morphometric ratios. However, since the latter method remains popular with some authors (especially in postcranial material: Samuels *et al.*, 2012; Meloro *et al.*, 2013), morphometric ratios were calculated as a 'test case' for British material from MIS 7, 5a and 3, to explore any temporal differences, as well as for species differentiation between *C. etruscus, C. arnensis, C. mosbachensis* and *C. lupus*.

Following Van Valkenburgh (1988a, 1989) and Van Valkenbrugh and Koepfli (1993) specific morphometric ratios describing the relative proportions of flesh, bone and non-flesh in diet were calculated. These included: premolar shape (PMD), relative blade length (RBL), relative lower molar grinding area (RLGA), and upper molar area (UM2/1). The relevant calculations shown in Table 4.5.

Ratio	Calculation
PMD	Ratio of maximum medio-lateral width to maximum antero-posterior length of p4
RBL	Ratio of m1 trigonid length to maximum antero-posterior length of m1

RLGA	Square root of the summed areas of the m1 talonid and m2, divided by length of m1 trigonid. Tooth area calculated as maximum width multiplied by maximum length.
UM2/1	Square root of M2 area divided by the square root of M1 area.

Table 4.5. Morphometric ratio calculation after Van Valkenburgh (1988a) and Van Valkenburgh and Koepfli (1993).

Premolar shape (PMD) determines the proportion of bone incorporated into the diet, on the basis that rounder premolars indicate a shift from a flesh-only diet (where premolars are narrow), to a diet incorporating more non-flesh and bone (Van Valkenburgh, 1988a, 1989).

Relative blade length (RBL) quantifies the relative proportion of the m1 devoted to a slicing function (m1 trigonid) as opposed to grinding (m1 talonid), and thus indicates the proportion of flesh incorporated into diet (Van Valkenburgh, 1988a).

Relative lower molar grinding area (RLGA) represents the proportion of the lower molar area functioning as a grinding mechanism as opposed to slicing of the m1 (Van Valkenburgh and Koepfli, 1993). Large grinding areas are indicative of higher proportions of non-flesh foods in diet. Similarly, the area of the upper molars (UM2/1) is also indicative of the proportion of non-flesh food able to be incorporated into diet.

One-way ANOVA was used to analyse the variance between the temporal groups of MIS 7, 5a and 3, as well as between the Pleistocene species groups of *C. etruscus, C. arnensis, C. mosbachensis* and *C. lupus*. Levene's test was used to test for the equality of variances for both analyses.

If a ratio was found to be significant, *post hoc* tests for multiple comparisons were used, such as Tukey HSD for ratios found to have equal variances, and Dunnett's T3 for those found to have unequal variances.

4.5.6. Tooth breakage and wear

Tooth breakage and wear was visually assessed for all species by site in both Britain and mainland Europe. A tooth was considered broken if subsequent wear during life was present, caused by tooth-tooth or tooth-food contact (Van Valkenburgh, 1988b; Van Valkenburgh and Hertel, 1993).

Following Binder et al. (2002), teeth were originally assigned a wear score of 1-5, based on W1: no apparent wear with no blunting of cusps, W2: slight wear only, W3: moderate wear, initial blunting of some cusps, W4: heavy wear, blunting of cusps apparent, and W5: severe

wear, with strongly blunted cusps. However, these categories were subsequently grouped with the more inclusive descriptors: *slight, moderate* and *heavy* after Van Valkenburgh (1988b) and Van Valkenburgh and Hertel (1993) to improve analysis by increasing tooth numbers in each category. The original wear scores were therefore amalgamated into the modified wear categories with W1-2 into *slight*, W3 as *moderate*, and W4-5 as *heavy*.

4.5.6.1. Two-way Chi-square test

The frequency of tooth breakage and wear was analysed using two-way Chi-square tests (Van Valkenburgh, 1988b), whereby the frequencies are classified according to two categories (Hawkins, 2009). Since this process aimed to explore whether temporal differences in tooth breakage and wear were present in the different canid species, the first category was age group, and the second either tooth breakage or tooth wear. The observed frequency distribution was then compared to the expected frequency distribution, which is based on the two sets of categories having no association (Hawkins, 2009).

For tooth breakage analysis, the data were organised into 2x2 contingency tables, showing single cell counts of each unbroken and broken tooth present in the analysed age group. For tooth wear analysis, the data were organised into 2x3 contingency tables and classified into the wear categories of slight, moderate and heavy.

The null hypothesis (H_0) for the test was that *there is no difference between the observed two-way frequency distribution and that expected based on no association between two sets of categories*. The critical significance level (α) = 0.05 for all Chi-square tests.

A Pearson Chi-square test was used in the analysis of tooth breakage. However, Fisher's exact test was used when one or more of the cells had an expected frequency of <5. The Chi-square test normally assumes that each cell has a frequency of >5, whereas Fisher's exact test does not make this assumption and can therefore be used with low expected frequencies.

Retention of the H_0 indicated that no differences were found between the observed frequency distribution and the expected frequency distribution. In contrast, rejection of the H_0 indicated that differences were found. An association between the age groups could then be tested and either tooth breakage or wear identified.

5. Results

5.1. Preliminary analysis of distribution, correlation and variation

5.1.1. MNI and NISP by site

As indicated in Chapter 4, the total number of Pleistocene specimens recorded was 5604, comprised of 4621 specimens of *C. lupus*, 666 of *C. mosbachensis*, 95 of *C. arnensis* and 222 specimens of *C. etruscus*.

The NISP (Number of Identifiable Specimens) and MNI (Minimum Number of Individuals) were calculated for each chronologically well-constrained site used in the analysis. Table 5.1 indicates the NISP and MNI for the British sites containing *C. lupus* and *C. mosbachensis* used in the analysis.

Site	Site code	Age (MIS)	Total NISP site	NISP strata	MNI *Canis*
Cae Gywn Cave	**CGC**	**2**	18		1
Ogof yr Ychen	**OGF**	**2**	23		1
Sun Hole	**SH**	**2**	18		1
Black Rock Quarry	**BRQ**	**3**	57		5
Kents Cavern (Cave Earth)	**KC**	**3**	143	140	6
Oreston Cave	**OSTN**	**3**	30		6
Paviland	**PAV**	**3**	62		10
Pin Hole Cave	**PHC**	**3**	97		5
Sandford Hill	**SFH**	**3**	41		1
Uphill Cave	**UPH**	**3**	32		1
Banwell Bone Cave	**BWL**	**5a**	557		21
Bosco's Den	**BSD**	**5a**	42		6
Steetley Quarry	**STQ**	**5a**	8		1
Stump Cross Cave	**SCC**	**5a**	32		1
Windy Knoll	**WK**	**5a**	149		4
Wretton	**WTN**	**5a**	33		2
Bacon Hole (upper layer)	**BH**	**5c**	7	5	1
Minchin Hole	**MCN**	**5c**	9		2
Picken's Hole (Layer 5)	**PKN**	**5c**	178	121	2
Barrington	**BTN**	**5e**	11		1
Joint Mitnor Cave	**JMC**	**5e**	378		2
Clevedon Cave	**CVD**	**6**	195		7
Crayford	**CYD**	**7**	24		4
Hutton Cave	**HTN**	**7**	202		5
Ilford	**ILF**	**7**	4		1
Marsworth	**MRSW**	**7**	52		4

Pontnewydd Cave (L. Breccia & Int. Layer)	**PNC**	**7**	396	181	2
Tornewton Cave (Otter Stratum)	**TNC OS**	**7**	1708	94	1
Grays Thurrock	**GYT**	**9**	7		1
Boxgrove	**BXG**	**13**	109		5
Sidestrand	**SSD**	**13**	2		1
Westbury-sub-Mendip	**WSM**	**13**	198		16
Overstrand	**OSD**	**15**	4		1
West Runton	**WRTN**	**17**	13		2

Table 5.1. MNI and NISP information for British sites used in the analysis. Site code indicated. Age of site or pertinent strata used in the analysis given. Total NISP indicates NISP for whole site, including all strata if relevant. NISP strata indicates NISP for specific strata of interest. MNI of *C. lupus* (MIS 2-7) and *C. mosbachensis* (MIS 9-17) given only.

The system of broad age groups for assemblages from European mainland sites was outlined in Chapter 4. Table 5.2 shows the NISP and MNI for dated sites from Italy and Germany, containing *C. lupus, C. mosbachensis, C. arnensis* and *C. etruscus*.

Site	Site code	Age group	Total NISP site	MNI Canis
Grotta di Paglicci	**PAG**	**2**	36	1
Perick Cave	**PRK**	**2.4**	10	5
Ranis	**RNS**	**2.4**	1	1
Villa Seckendorf, Bad Canstatt	**BCT**	**2.8**	39	6
Taubach	**TBH**	**2.8**	12	1
Monte Tignoso	**MTG**	**2.8**	2	1
Dobelhaldeschacht	**DBL**	**3**	6	1
Weimar-Ehringsdorf	**WEHF**	**3**	9	2
Cengelle II	**CGL**	**3.4**	23	2
Heppenloch	**HPN**	**3.4**	5	1
Monte Zoppega	**ZPG**	**3.4**	5	2
Voigtstedt	**VOI**	**3.8**	8	1
Viatelle	**VIA**	**4**	15	2
Untermassfeld	**UMF**	**4**	277	12
Upper Valdarno Basin	**UV**	**4.4**	161	8 (C.a), 14 (C.e)
Val di Magra	**OLV**	**4.4**	156	7

Table 5.2. MNI and NISP information for European sites used in the analysis. Site code and age of the site given. Total NISP indicates NISP for the whole site, including all strata where relevant. MNI of *C. lupus* (age groups 2-3) and *C. mosbachensis* (age groups 3.4-4), *C. arnensis* (UV only, age group 4.4) and *C. etruscus* (age group 4.4) are given only.

5.1.2. Outliers and Shapiro-Wilk test for normality

Using histograms and Q-Q plots, outliers were identified and removed from the dataset, after which the Shapiro-Wilk test for normality was employed on all raw measurements, based on species groups (see Chapter 4).

5.1.2.1. Shapiro-Wilk tests: *Canis lupus*

Table 5.3 presents the results for Shapiro-Wilk tests of normality for *C. lupus* from Pleistocene sites of Britain and European mainland, and including modern European *C. lupus*. All measurements have a not non-normal distribution (p>0.05) and normality is therefore inferred.

Measure	*Canis lupus*						
	n	Mean	SE mean	SD	*W* Statistic	df	*p*
p4L	132	16.02	0.078	0.895	0.984	132	0.117
p4W	132	8.16	0.055	0.633	0.983	132	0.101
m1L	128	29.18	0.139	1.567	0.989	128	0.432
m1Ltrig	128	20.46	0.104	1.181	0.993	128	0.820
m1Ltal	127	7.61	0.056	0.634	0.987	127	0.269
m1W	128	11.69	0.066	0.744	0.994	128	0.865
m2L	109	11.74	0.074	0.776	0.987	109	0.351
m2W	109	8.87	0.060	0.631	0.989	109	0.555
p1p4L	95	50.38	0.276	2.687	0.982	95	0.218
p2p4L	101	43.82	0.229	2.304	0.987	101	0.456
p1m3L	77	95.66	0.408	3.578	0.985	77	0.476
p2m3L	78	89.17	0.398	3.515	0.986	78	0.531
DentaryL	64	174.83	1.209	9.673	0.978	64	0.324
p3p4D	100	27.52	0.231	2.314	0.984	100	0.270
p3p4B	94	12.78	0.133	1.285	0.986	94	0.449
m1m2D	93	32.07	0.315	3.038	0.990	93	0.745
m1m2B	91	13.03	0.128	1.225	0.987	91	0.498
P3L	85	15.95	0.120	1.108	0.992	85	0.901
P4L	79	26.35	0.155	1.379	0.985	79	0.513
P4W	78	14.03	0.127	1.119	0.991	78	0.851
M1L	107	16.61	0.101	1.041	0.985	107	0.254
M1W	99	22.38	0.158	1.573	0.992	99	0.790
M2W	76	14.10	0.103	0.901	0.979	76	0.244
P1P4L	64	64.03	0.464	3.716	0.971	64	0.130
P1M2L	61	83.73	0.472	3.688	0.990	61	0.888
C1M2L*	59	86.35	0.511	3.925	0.969	59	0.143
M1M2L	81	23.15	0.189	1.699	0.973	81	0.083

Table 5.3. Results from Shapiro-Wilk tests of *C. lupus* from Britain and Europe, Pleistocene and recent. Raw measurements, L: length, W: width, B: breadth, D: depth, trig: trigonid, tal: talonid. *no corresponding European measurement. Significance indicated by p<0.05.

5.1.2.2. Shapiro-Wilk tests: *Canis mosbachensis*

Table 5.4 indicates the results from Shapiro-Wilk tests for *C. mosbachensis* from sites of Britain and Europe of Pleistocene age. Any identified outliers have been removed. All measurements have a not non-normal distribution (p>0.05) and normality is therefore inferred.

Measure	*Canis mosbachensis*						
	n	**mean**	**SE mean**	**SD**	***W* statistic**	**df**	***p***
p4L	24	13.69	0.194	0.950	0.921	24	0.060
p4W	24	6.28	0.131	0.640	0.920	24	0.058
m1L	24	24.11	0.239	1.169	0.940	24	0.162
m1Ltrig	26	16.24	0.200	1.020	0.977	26	0.817
m1Ltal	29	6.71	0.073	0.393	0.963	29	0.392
m1W	24	9.23	0.126	0.616	0.972	24	0.724
m2L	28	10.20	0.169	0.894	0.973	28	0.656
m2W	25	7.57	0.137	0.687	0.977	25	0.829
p1p4L	12	43.17	0.514	1.779	0.890	12	0.118
p2p4L	18	38.22	0.676	2.867	0.962	18	0.642
p1m3L	9	82.30	0.886	2.657	0.990	9	0.995
p2m3L	12	77.20	0.874	3.027	0.921	12	0.293
DentaryL	5	132.04	1.755	3.925	0.967	5	0.855
p3p4D	18	19.68	0.615	2.607	0.901	18	0.059
p3p4B	18	9.19	0.294	1.245	0.904	18	0.068
m1m2D	15	22.14	0.547	2.119	0.940	15	0.377
m1m2B	15	10.01	0.216	0.835	0.977	15	0.942
P3L	11	13.55	0.249	0.826	0.956	11	0.719
P4L	16	22.57	0.290	1.161	0.957	16	0.608
P4W	14	11.00	0.213	0.796	0.957	14	0.679
M1L	22	13.60	0.154	0.724	0.975	22	0.814
M1W	19	18.66	0.263	1.147	0.954	19	0.456
M2L	15	7.62	0.229	0.887	0.975	15	0.923
M2W	15	12.13	0.282	1.092	0.967	15	0.809
P1P4L	4	57.99	1.329	2.658	0.852	4	0.232
P1M2L	3	75.85	1.318	2.284	0.794	3	0.100
C1M2L	3	77.36	1.794	3.107	0.838	3	0.209
M1M2L	8	19.76	0.443	1.253	0.959	8	0.805

Table 5.4. Results from Shapiro-Wilk test for *C. mosbachensis* from Britain and Europe Pleistocene sites. Raw measurements, L: length, W: width, B: breadth, D: depth, trig: trigonid, tal: talonid, mand: mandible. Significance indicated by p<0.05.

5.1.2.3. Shapiro-Wilk tests: *Canis etruscus*

Table 5.5 indicates the results from Shapiro Wilk tests for *C. etruscus* from European sites. Any identified outliers have been removed. All measurements have a not non-normal distribution (p>0.05) and normality is thus inferred.

Measure	*Canis etruscus*						
	n	**mean**	**SE mean**	**SD**	***W* Statistic**	**df**	***p***

p4L	16	15.12	0.163	0.651	0.924	16	0.199
p4W	15	6.88	0.104	0.401	0.981	15	0.975
m1L	16	25.06	0.287	1.147	0.951	16	0.505
m1Ltrig	14	16.94	0.256	0.960	0.949	14	0.542
m1Ltal	15	6.89	0.081	0.312	0.888	15	0.062
m1W	15	9.64	0.100	0.389	0.892	15	0.071
m2L	15	11.04	0.188	0.729	0.935	15	0.326
m2W	12	7.87	0.124	0.429	0.967	12	0.876
p1p4L	11	48.30	0.707	2.346	0.898	11	0.175
p2p4L	12	41.22	0.576	1.997	0.940	12	0.498
p1m3L	8	88.67	1.449	4.098	0.872	8	0.157
p2m3L	9	82.41	1.334	4.002	0.922	9	0.406
DentaryL	3	142.28	7.666	13.277	0.797	3	0.108
p3p4D	13	21.35	0.677	2.436	0.936	13	0.404
p3p4B	13	9.88	0.281	1.014	0.957	13	0.704
m1m2D	14	24.56	0.612	2.288	0.955	14	0.648
m1m2B	11	10.61	0.097	0.321	0.967	11	0.851
P3L	5	14.26	0.060	0.134	0.844	5	0.177
P4L	8	22.29	0.479	1.356	0.977	8	0.944
P4W	8	11.42	0.306	0.867	0.916	8	0.397
M1L	9	15.56	0.217	0.652	0.940	9	0.577
M1W	9	20.33	0.328	0.985	0.973	9	0.916
M2L	6	7.77	0.138	0.338	0.991	6	0.992
M2W	5	12.35	0.333	0.745	0.964	5	0.833
P1P4L	N/A						
P1M2L	N/A						
C1M2L	N/A						
M1M2L	4	21.67	1.034	2.069	0.943	4	0.676

Table 5.5. Results from Shapiro-Wilk tests for *C. etruscus* from Europe Pleistocene. Raw measurements, L: length, W: width, B: breadth, D: depth, trig: trigonid, tal: talonid. N/A no measurement possible. Significance indicated by $p<0.05$.

5.1.2.4. Shapiro-Wilk tests: *Canis arnensis*

Table 5.6 indicates the results from Shapiro-Wilk tests for *C. arnensis* from European sites of Pleistocene age. Any identified outliers have been removed. All measurements have a not non-normal distribution ($p>0.05$) and normality is therefore inferred.

Measure	***Canis arnensis***						
	n	**mean**	**SE mean**	**SD**	***W* Statistic**	**df**	***p***
p4L	11	13.22	0.146	0.484	0.950	11	0.641
p4W	11	5.78	0.098	0.326	0.906	11	0.218
m1L	10	21.93	0.334	1.056	0.903	10	0.236
m1Ltrig	10	14.64	0.201	0.635	0.934	10	0.490
m1Ltal	10	6.29	0.143	0.453	0.913	10	0.301
m1W	9	8.36	0.132	0.396	0.915	9	0.351
m2L	10	10.15	0.210	0.663	0.977	10	0.946
m2W	8	7.08	0.189	0.535	0.989	8	0.994
p1p4L	6	43.90	0.689	1.688	0.941	6	0.667
p2p4L	7	37.90	0.671	1.775	0.891	7	0.281
p1m3L	4	79.59	1.594	3.189	0.881	4	0.345
p2m3L	6	73.87	1.386	3.396	0.891	6	0.324

DentaryL	N/A						
p3p4D	7	18.37	0.775	2.051	0.927	7	0.524
p3p4B	5	7.99	0.064	0.144	0.928	5	0.580
m1m2D	7	21.34	0.718	1.900	0.916	7	0.439
m1m2B	6	9.09	0.396	0.970	0.950	6	0.743
P3L	3	12.17	0.288	0.500	0.923	3	0.463
P4L	4	20.17	0.154	0.309	0.931	4	0.603
P4W	4	9.61	0.351	0.703	0.971	4	0.847
M1L	5	13.10	0.385	0.862	0.863	5	0.240
M1W	5	17.74	0.413	0.924	0.883	5	0.321
M2L	4	6.89	0.130	0.260	0.776	4	0.065
M2W	4	11.51	0.290	0.579	0.788	4	0.082
P1P4L	3	54.39	0.061	0.106	0.981	3	0.739
P1M2L	3	70.88	0.335	0.580	0.998	3	0.924
C1M2L	3	73.09	1.368	2.370	0.901	3	0.389
M1M2L	4	18.23	0.135	0.269	0.890	4	0.384

Table 5.6. Results from Shapiro-Wilk tests for *C. arnensis* from Europe Pleistocene. Raw measurements, L: length, W: width, B: breadth, D: depth, trig: trigonid, tal: talonid. N/A no measurement possible. Significance indicated by $p<0.05$.

5.1.2.5. Shapiro-Wilk tests: *Canis adustus*

As mentioned in Chapter 4, an additional 235 individuals of modern extant canids were recorded, of which *C. adustus, C. aureus, C. mesomelas, C. alpinus* and *L. pictus* were included for comparison with *C. lupus* and the Pleistocene canids in terms of dietary analysis. For the dietary analysis, the presence of outliers was identified using histograms and Q-Q plots, and the numerical distribution of the measurements was examined using Shapiro-Wilk tests.

Table 5.7 indicates the results from Shapiro-Wilk tests for the modern *C. adustus* group. Any identified outliers have been removed. All measurements have a not non-normal distribution ($p>0.05$) and normality is inferred.

Measure	***Canis adustus***						
	n	**mean**	**SE mean**	**SD**	***W* Statistic**	**df**	***p***
p4L	25	10.12	0.089	0.447	0.969	25	0.619
p4W	25	4.39	0.056	0.279	0.967	25	0.579
m1L	21	17.05	0.083	0.380	0.952	21	0.370
m1Ltrig	24	10.45	0.125	0.612	0.962	24	0.477
m1Ltal	24	5.90	0.095	0.467	0.978	24	0.866
m1W	25	6.78	0.119	0.593	0.979	25	0.866
m2L	25	9.34	0.123	0.614	0.988	25	0.987
m2W	24	6.48	0.100	0.490	0.964	24	0.526
p1p4L	26	34.39	0.340	1.736	0.973	26	0.713
p2p4L	26	29.07	0.325	1.657	0.968	26	0.578
p1m3L	26	65.17	0.582	2.958	0.932	26	0.085
p2m3L	26	60.00	0.523	2.669	0.948	26	0.207
DentaryL	26	116.80	1.184	6.036	0.987	26	0.981

p3p4D	26	13.38	0.152	0.774	0.979	26	0.843
p3p4B	26	6.56	0.094	0.479	0.924	26	0.057
m1m2D	26	14.92	0.191	0.972	0.967	26	0.536
m1m2B	26	6.89	0.130	0.662	0.937	26	0.114
P3L	25	9.17	0.147	0.736	0.968	25	0.593
P4L	26	15.61	0.216	1.101	0.953	26	0.269
P4W	25	7.43	0.092	0.458	0.967	25	0.571
M1L	26	11.88	0.163	0.832	0.930	26	0.077
M1W	25	14.93	0.201	1.004	0.984	25	0.956
M2L	26	7.65	0.189	0.961	0.927	26	0.064
M2W	26	10.56	0.182	0.929	0.968	26	0.581
P1P4L	26	40.36	0.460	2.343	0.958	26	0.352
P1M2L	26	56.60	0.517	2.365	0.964	26	0.482
C1M2L	26	61.03	0.553	2.819	0.934	26	0.095
M1M2L	24	18.45	0.184	0.903	0.923	24	0.068

Table 5.7. Results from Shapiro-Wilk tests for the modern *Canis adustus* group. Raw measurements, L: length, W: width, B: breadth, D: depth, trig: trigonid, tal: talonid. Significance indicated by $p<0.05$.

5.1.2.6. Shapiro-Wilk tests: *Canis aureus*

Table 5.8 indicates the results from Shapiro Wilk tests for the recent *C. aureus* group. Any identified outliers have been removed. All measurements have a not non-normal distribution ($p>0.05$) and normality is inferred.

Measure	*Canis aureus*						
	n	mean	SE mean	SD	*W* Statistic	df	*p*
p4L	31	10.15	0.115	0.639	0.959	31	0.271
p4W	31	4.75	0.066	0.366	0.969	31	0.491
m1L	30	17.90	0.212	1.159	0.964	30	0.389
m1Ltrig	30	11.79	0.161	0.882	0.947	30	0.139
m1Ltal	31	5.76	0.087	0.483	0.961	31	0.319
m1W	30	6.83	0.105	0.575	0.943	30	0.108
m2L	30	8.59	0.145	0.795	0.977	30	0.745
m2W	30	6.04	0.076	0.417	0.971	30	0.580
p1p4L	30	33.56	0.331	1.811	0.944	30	0.116
p2p4L	30	29.15	0.247	1.355	0.965	30	0.415
p1m3L	30	64.00	0.599	3.281	0.969	30	0.518
p2m3L	31	59.00	0.546	3.037	0.968	31	0.466
DentaryL	31	109.68	0.878	4.889	0.965	31	0.388
p3p4D	31	14.24	0.216	1.205	0.964	31	0.370
p3p4B	31	6.73	0.103	0.574	0.939	31	0.078
m1m2D	30	16.22	0.257	1.409	0.947	30	0.143
m1m2B	30	7.16	0.128	0.702	0.954	30	0.215
P3L	31	9.83	0.120	0.669	0.957	31	0.235
P4L	30	16.28	0.186	1.021	0.963	30	0.364
P4W	31	8.15	0.142	0.791	0.962	31	0.321
M1L	29	11.31	0.145	0.783	0.945	29	0.132
M1W	29	14.92	0.183	0.984	0.970	29	0.567
M2L	31	6.50	0.100	0.555	0.953	31	0.187
M2W	29	10.17	0.113	0.608	0.946	29	0.144

P1P4L	31	41.47	0.412	2.291	0.973	31	0.603
P1M2L	31	55.92	0.508	2.831	0.957	31	0.249
C1M2L	31	57.79	0.504	2.804	0.983	31	0.892
M1M2L	31	16.09	0.208	1.156	0.964	31	0.373

Table 5.8. Results from Shapiro-Wilk tests for recent *Canis aureus* group. Raw measurements, L: length, W: width, B: breadth, D: depth, trig: trigonid, tal: talonid. Significance indicated by $p<0.05$.

5.1.2.7. Shapiro-Wilk tests: *Canis mesomelas*

Table 5.9 indicates the results from Shapiro Wilk tests for the modern *C. mesomelas* group. Any identified outliers have been removed. All measurements have a not non-normal distribution ($p>0.05$) and normality is inferred.

Measure	*Canis mesomelas*						
	n	mean	SE mean	SD	*W* Statistic	df	*p*
p4L	29	9.96	0.104	0.562	0.937	29	0.084
p4W	29	4.39	0.046	0.245	0.945	29	0.139
m1L	29	18.23	0.189	1.020	0.973	29	0.647
m1Ltrig	29	11.87	0.140	0.753	0.966	29	0.466
m1Ltal	29	5.70	0.060	0.322	0.958	29	0.299
m1W	29	7.12	0.103	0.556	0.970	29	0.559
m2L	25	8.06	0.120	0.602	0.973	25	0.718
m2W	25	6.04	0.098	0.488	0.965	25	0.531
p1p4L	29	32.62	0.318	1.711	0.981	31	0.859
p2p4L	29	27.58	0.295	1.590	0.970	29	0.567
p1m3L	29	62.59	0.529	2.849	0.946	29	0.142
p2m3L	29	57.65	0.502	2.701	0.962	29	0.359
DentaryL	29	107.78	0.949	5.111	0.970	29	0.552
p3p4D	27	13.05	0.171	0.887	0.930	27	0.068
p3p4B	29	6.65	0.091	0.492	0.978	29	0.798
m1m2D	28	15.33	0.164	0.866	0.967	28	0.504
m1m2B	29	7.10	0.093	0.503	0.967	29	0.477
P3L	29	9.24	0.123	0.662	0.958	29	0.286
P4L	30	16.97	0.170	0.930	0.973	30	0.619
P4W	30	7.79	0.106	0.581	0.958	30	0.278
M1L	30	11.24	0.111	0.609	0.964	30	0.386
M1W	29	15.11	0.125	0.672	0.975	29	0.699
M2L	30	6.23	0.104	0.572	0.944	30	0.114
M2W	30	10.22	0.104	0.572	0.965	30	0.424
P1P4L	30	42.03	0.441	2.415	0.975	30	0.678
P1M2L	30	55.93	0.483	2.643	0.981	30	0.842
C1M2L	30	58.36	0.496	2.716	0.949	30	0.156
M1M2L	30	16.00	0.146	0.799	0.981	30	0.860

Table 5.9. Results from Shapiro-Wilk tests for recent *Canis mesomelas* group. Raw measurements, L: length, W: width, B: breadth, D: depth, trig: trigonid, tal: talonid. Significance indicated by $p<0.05$.

5.1.2.8. Shapiro-Wilk tests: *Cuon alpinus*

Table 5.10 indicates the results from Shapiro Wilk tests for the modern *C. alpinus* group. Any identified outliers have been removed. All measurements have a not non-normal distribution (p>0.05) and normality is inferred.

Measure	*Cuon alpinus*						
	n	**mean**	**SE mean**	**SD**	***W* Statistic**	**df**	***p***
p4L	28	12.33	0.123	0.649	0.970	28	0.580
p4W	28	6.04	0.076	0.403	0.981	28	0.878
m1L	28	21.37	0.172	0.909	0.963	28	0.407
m1Ltrig	28	15.16	0.155	0.820	0.984	28	0.937
m1Ltal	28	5.39	0.065	0.343	0.949	28	0.182
m1W	28	8.23	0.077	0.410	0.930	28	0.062
m2L	22	7.04	0.089	0.416	0.926	22	0.101
m2W	26	6.00	0.054	0.277	0.948	26	0.204
p1p4L	28	37.60	0.366	1.938	0.966	28	0.476
p2p4L	28	31.53	0.309	1.633	0.970	28	0.581
p1m3L	N/A						
p2m3L	N/A						
DentaryL	28	128.62	1.163	6.155	0.974	28	0.692
p3p4D	28	19.12	0.308	1.630	0.975	28	0.732
p3p4B	28	9.83	0.100	0.528	0.952	28	0.216
m1m2D	27	22.99	0.276	1.435	0.979	27	0.832
m1m2B	27	9.45	0.098	0.510	0.976	27	0.771
P3L	27	11.04	0.102	0.531	0.976	27	0.765
P4L	30	20.26	0.169	0.926	0.960	30	0.316
P4W	25	10.22	0.085	0.423	0.950	25	0.244
M1L	29	12.69	0.152	0.817	0.946	29	0.148
M1W	30	15.56	0.128	0.703	0.982	30	0.867
M2L	23	4.28	0.141	0.675	0.927	23	0.096
M2W	23	7.23	0.198	0.949	0.956	23	0.390
P1P4L	30	47.59	0.424	2.321	0.962	30	0.357
P1M2L	28	60.90	0.462	2.444	0.967	28	0.510
C1M2L	28	62.55	0.479	2.536	0.972	28	0.636
M1M2L	29	15.58	0.165	0.888	0.955	29	0.244

Table 5.10. Results from Shapiro-Wilk tests for the modern *Cuon alpinus* group. Raw measurements, L: length, W: width, B: breadth, D: depth, trig: trigonid, tal: talonid. N/A no measurement possible. Significance indicated by p<0.05.

5.1.2.9. Shapiro-Wilk tests: *Lycaon pictus*

Table 5.11 indicates the results from Shapiro Wilk tests for the modern *L. pictus* group. Any identified outliers have been removed. All measurements have a not non-normal distribution (p>0.05) and normality is inferred.

Measure	*Lycaon pictus*						
	n	**mean**	**SE mean**	**SD**	***W* Statistic**	**df**	***p***
p4L	26	13.14	0.158	0.807	0.948	26	0.209
p4W	26	6.51	0.103	0.523	0.984	26	0.939
m1L	27	24.43	0.227	1.181	0.992	27	0.999
m1Ltrig	26	16.78	0.109	0.555	0.948	26	0.208

m1Ltal	27	6.71	0.081	0.418	0.974	27	0.702
m1W	27	9.46	0.099	0.509	0.933	27	0.081
m2L	27	10.02	0.122	0.634	0.946	27	0.171
m2W	27	7.25	0.079	0.411	0.963	27	0.439
p1p4L	27	41.67	0.362	1.882	0.974	27	0.706
p2p4L	27	34.80	0.321	1.667	0.970	27	0.602
p1m3L	25	79.52	0.672	3.358	0.985	25	0.963
p2m3L	24	72.96	0.655	3.210	0.964	24	0.532
DentaryL	26	143.51	1.176	6.000	0.951	26	0.245
p3p4D	27	21.64	0.336	1.745	0.962	27	0.413
p3p4B	27	10.92	0.156	0.809	0.969	27	0.573
m1m2D	27	25.98	0.356	1.847	0.987	27	0.974
m1m2B	27	11.35	0.182	0.944	0.936	27	0.095
P3L	27	11.99	0.094	0.489	0.962	27	0.409
P4L	26	21.10	0.184	0.938	0.964	26	0.481
P4W	26	11.00	0.135	0.689	0.967	26	0.548
M1L	27	15.80	0.138	0.716	0.952	27	0.239
M1W	27	18.22	0.175	0.908	0.960	27	0.373
M2L	19	7.48	0.098	0.425	0.919	19	0.110
M2W	27	9.71	0.171	0.888	0.968	27	0.538
P1P4L	27	50.29	0.438	2.277	0.959	27	0.304
P1M2L	27	68.78	0.522	2.713	0.960	27	0.368
C1M2L	26	69.69	0.680	3.466	0.929	26	0.072
M1M2L	27	21.12	0.185	0.961	0.983	27	0.926

Table 5.11. Results from Shapiro-Wilk tests for the modern *Lycaon pictus* group. Raw measurements, L: length, W: width, B: breadth, D: depth, trig: trigonid, tal: talonid. Table Significance indicated by $p<0.05$.

5.1.3. Correlations between measurements

The presence of linear correlations between the measurements was investigated in the *C. lupus* dataset (including British Pleistocene and European mainland material, as well as modern European wolves). Due to lower numbers of individuals in the *C. mosbachensis, C. etruscus* and *C. arnensis* datasets, various measurements could not be statistically tested. However, since all are members of *Canis* and share broadly similar dental morphology, it was considered reasonable to use the results of the correlations in the measurements of the *C. lupus* dataset as a proxy for other members of the genus.

The presence of correlations between measurements was tested using the parametric Pearson product moment correlation. Table 5.12 reveals that many of the significant correlations are weak, either negatively or positively. Summarised here are the significant ($p<0.05$) strong positive correlations (no strong negative correlations were found): p4L has a strong positive correlation to p4W ($r_{129} = 0.691$, $p = 0.0001$), m1L has a strong positive correlation to m1Ltrig ($r_{126} = 0.835$, $p=0.0001$), m1Ltal $r_{125} = 0.560$, $p=0.0001$) and m1W ($r_{126} = 0.819$, $p=0.0001$).

Measure	p4L	p4W	m1L	m1trig	m1tal	m1W	m2L	m2W	p1p4L	p2p4L	p3m3L	p2m3L	DentaryL	p3p4D	p3p4B	m1m2D	m1m2B	P3L	P4L	P4W	M1L	M1W	M2W	P1P4L	P1M2L	C1M2L	M1M2L
p4L		r_{139}=0.691, p=0.0001	r_{123}= -0.034, p=0.708	r_{123}=0.096, p=0.281	r_{124}= 0.215, p=0.015	r_{125}=0.091 p=0.307	r_{106}=-0.213 p=0.027	r_{106}= -0.109 p=0.263	r92 =-0.143 p=0.170	r98 =0.059 p=0.558	r74 = 0.056 p=0.629	r75 =-0.064 p=0.581	r61 =-0.051, p=0.694	r96 = 0.331, p=0.001	r91=0.235, p=0.023	r90 = 0.387, p=0.0001	r88 = 0.186, p=0.079	r82 = 0.087, p=0.431	r76 = 0.171, p=0.133	r75 = 0.136, p=0.237	r104 =-0.225, p=0.020	r96 =-0.304, p=0.002	r74 =0.082, p=0.480	r61 = 0.158, p=0.215	r58 =0.118, p=0.370	r56 =-0.076, p=0.571	r78=0.048, p=0.675
p4W			r124= -0.001, p=0.989	r_{124}=0.124, p=0.166	r_{125}= -0.198, p=0.027	r_{126}=0.120, p=0.183	r_{126}=-0.069, p=0.479	r_{106}=0.014, p=0.886	r91= 0.185, p=0.076	r97=-0.011, p=0.913	r73=-0.146, p=0.212	r74 =-0.107, p=0.358	r62 =-0.227p=0.071	r95 =-0.106, p=0.301	r90 =-0.273, p=0.008	r89 =-0.393, p=0.0001	r87 =-0.211, p=0.048	r81 =-0.079, p=0.479	r75 =-0.298, p=0.008	r74 =-0.388, p=0.001	r103 =-0.229, p=0.019	r95 =-0.178, p=0.081	r73 =-0.022, p=0.855	r62 =-0.192, p=0.129	r59 =-0.125, p=0.339	r57 =0.001, p=0.993	r77=-0.069, p=0.546
m1L				r_{124}=0.835, p=0.0001	r_{125}=0.560, p=0.0001	r_{126}=0.819, p=0.0001	r107 =-0.033, p=0.736	r107 =-0.071, p=0.465	r93 =0.058 p=0.577	r99 =0.013 p=0.900	r75 =-0.236, p=0.039	r74 =-0.164, p=0.152	r62 =0.166, p=0.190	r97 =0.074, p=0.468	r92 =-0.212, p=0.040	r91 = -0.176, p=0.092	r89 = -0.155, p=0.141	r83 = -0.153, p=0.163	r77 = -0.183, p=0.107	r76 = -0.209, p=0.067	r105 = 0.016 p=0.867	r97 = -0.060 p=0.556	r75 = -0.097 p=0.400	r62= 0.086 p=0.499	r59= 0.080 p=0.540	r57 = -0.142. p=0.283	r79= -0.198. p=0.076
m1trig					r125 =0.331, p=0.0001	r126 = 0.800, p=0.0001	r107 = -0.030, p=0.761	r107 = -0.061, p=0.526	r93 =0.041, p=0.693	r99 = 0.018, p=0.854	r75 = 0.270, p=0.018	r76 =-0.273, p=0.016	r62=0.002, p=0.989	r97=0.005, p=0.962	r92=0.176, p=0.089	r91=0.178, p=0.089	r89=-0.077, p=0.468	r83=0.122, p=0.265	r77=-0.285, p=0.011	r76=-0.283, p=0.012	r105 = -0.061 p=0.532	r97 = -0.183 p=0.069	r75 = -0.170 p=0.140	r62 = -0.024, p=0.849	r59 = 0.158, p=0.224	r57 = -0.258, p=0.048	r79= -0.188, p=0.093
m1tal						r125 =0.409, p=0.0001	r106 =-0.037, p=0.706	r106 =-0.018, p=0.850	r92 =-0.029, p=0.781	r98 = 0.109, p=0.281	r74 = -0.071, p=0.542	r75 =-0.094, p=0.415	r61 = 0.129, p=0.313	r96 = 0.220, p=0.030	r91=0.070, p=0.506	r90=0.112, p=0.286	r88=0.100, p=0.347	r82=-0.133, p=0.226	r76=0.065, p=0.570	r75=-0.033, p=0.778	r104 = 0.065, p=0.509	r96 = 0.009, p=0.929	r74 = 0.1 p=0.208	r61 = 0.178, p=0.162	r58 = 0.043, p=0.745	r56 = -0.101, p=0.451	r78 = -0.090, p=0.426
m1W							r107 = 0.054, p=0.574	r107 = 0.151, p=0.116	r93 = 0.066, p=0.526	r99 = -0.130, p=0.196	r75 = -0.119, p=0.302	r76 = -0.296, p=0.009	r62 = -0.055, p=0.664	r97 = -0.051, p=0.615	r92 = -0.175, p=0.091	r91 = -0.203, p=0.051	r89 = -0.060, p=0.572	r83 = -0.156, p=0.153	r77 = -0.252, p=0.025	r76 = -0.260, p=0.022	r105 = 0.113, p=0.247	r97 = 0.013, p=0.898	r75 = -0.067, p=0.563	r62 = -0.004, p=0.977	r59 = 0.087, p=0.506	r57 = -0.098, p=0.462	r79 = -0.128, p=0.254
m2L								r$_{106}$=0.665, p<0.0001	r91 = 0.073, p=0.486	r97 = -0.126, p=0.215	r74 = 0.186, p=0.107	r75 = 0.110, p=0.343	r61 = -0.007, p=0.956	r95 = 0.071, p=0.488	r90 = 0.158, p=0.132	r89 = 0.028, p=0.791	r87 = 0.048, p=0.658	r81 = -0.025, p=0.824	r76 = 0.065, p=0.574	r75 = -0.016, p=0.891	r103 = 0.138, p=0.160	r95 = 0.191, p=0.061	r74 = 0.094, p=0.420	r61 = 0.087, p=0.496	r58 = 0.057, p=0.665	r57 = 0.009, p=0.948	r78 = 0.045, p=0.689
m2W									r91 = 0.102, p=0.330	r97 = -0.052, p=0.612	r73 = 0.071, p=0.543	r74 = -0.029, p=0.805	r60 = -0.117, p=0.367	r95 = 0.057, p=0.576	r90 = 0.109, p=0.301	r89 = -0.046, p=0.665	r87 = 0.050, p=0.640	r81 = 0.046, p=0.681	r75 = -0.001, p=0.992	r74 = -0.107, p=0.358	r103 = 0.204, p=0.037	r96 = 0.163, p=0.108	r74 = 0.023, p=0.841	r60 = 0.030, p=0.817	r57 = -0.128, p=0.334	r55 = 0.087, p=0.522	r77 = -0.093, p=0.417
p1p4L										r93 = -0.086, p=0.406	r75 = 0.159, p=0.168	r76 = 0.189, p=0.098	r62 = -0.050, p=0.695	r93 = 0.100, p=0.333	r92 = 0.038, p=0.718	r91 = 0.051, p=0.628	r89 = 0.120 p=0.258	r83 = 0.142 p=0.196	r77 = 0.054 p=0.639	r76 = 0.118 p=0.303	r93 = 0.004, p=0.966	r85 = 0.020, p=0.856	r75 = 0.056, p=0.631	r62 = 0.030, p=0.812	r59 = -0.042, p=0.747	r57 = -0.076, p=0.565	r79 = 0.026, p=0.820
p2p4L											r75 = -0.200, p=0.082	r76 = 0.165, p=0.149	r62 = -0.207, p=0.101	r97 = 0.123, p=0.224	r92 = -0.094, p=0.366	r91 = 0.004, p=0.967	r89 = 0.238, p=0.023	r83 = -0.042 p=0.703	r77 = -0.163 p=0.150	r76 = 0.033 p=0.774	r99 = 0.020 p=0.845	r91 = 0.088, p=0.403	r75 = -0.010, p=0.934	r62 = 0.059, p=0.645	r59 = -0.323, p=0.011	r57 = -0.003, p=0.984	r79 = -0.097, p=0.388
p1m3L												r75 = 0.376, p=0.001	r62 = -0.002, p=0.988	r75 = -0.239, p=0.036	r75 = 0.007, p=0.952	r75 = 0.144, p=0.211	r75 = 0.149, p=0.196	r75 = -0.126, p=0.275	r74 = 0.233, p=0.043	r73 = 0.316, p=0.006	r75 = 0.029, p=0.803	r67 = 0.112, p=0.360	r72 = 0.206, p=0.079	r62 = 0.090, p=0.480	r59 = 0.045, p=0.728	r57 = 0.268, p=0.040	r75 = 0.246, p=0.031
p2m3L													r62 = 0.038, p=0.767	r76 = -0.126, p=0.270	r76 = -0.092, p=0.423	r76 = 0.086, p=0.452	r76 = 0.005, p=0.969	r76 = -0.056, p=0.629	r75 = 0.215, p=0.061	r74 = 0.208, p=0.071	r76 = -0.052, p=0.653	r68 = 0.112, p=0.355	r73 = 0.112, p=0.339	r62 = 0.124, p=0.327	r79 = -0.073, p=0.577	r57 = 0.073, p=0.582	r76 = 0.115, p=0.317
DentaryL														r62 = -0.210, p=0.095	r62 = -0.025, p=0.842	r62 = 0.036, p=0.779	r62 = -0.138, p=0.277	r62 = -0.058, p=0.650	r61 = 0.242, p=0.056	r60 = 0.244, p=0.056	r62 = 0.146, p=0.250	r54 = -0.135, p=0.323	r59 = 0.176, p=0.174	r62 = 0.342, p=0.006	r59 = 0.421, p=0.001	r57 = 0.238, p=0.069	r62 = 0.128, p=0.312
p3p4D															r$_{62}$=0.239, p=0.020	r91 = 0.231, p=0.026	r89 = 0.077, p=0.465	r83 = 0.031, p=0.775	r77 = 0.068, p=0.553	r76 = -0.162, p=0.155	r97 = 0.092, p=0.367	r89 = 0.125, p=0.237	r75 = -0.155, p=0.177	r62 = -0.307, p=0.014	r59 = -0.334, p=0.009	r57 = -0.211, p=0.108	r79 = -0.175, p=0.119
p3p4B																r91 = 0.339, p=0.001	r89 = 0.201, p=0.056	r83 = 0.096, p=0.381	r77 = 0.151, p=0.183	r76 = -0.021, p=0.857	r92 = 0.081, p=0.438	r84 = 0.134, p=0.218	r75 = -0.260, p=0.022	r62 = -0.145, p=0.252	r59 = -0.001, p=0.996	r57 = -0.218, p=0.097	r79 = 0.037, p=0.744
m1m2D																	r89 = 0.323, p=0.002	r83 = 0.117, p=0.286	r77 = 0.050, p=0.663	r76 = 0.121, p=0.290	r91 = 0.112, p=0.285	r83 = 0.073, p=0.508	r75 = -0.043, p=0.709	r62 = 0.019, p=0.879	r59 = -0.062, p=0.635	r57 = -0.147, p=0.266	r79 = 0.044, p=0.694
m1m2B																		r83 = 0.079, p=0.472	r77 = 0.139, p=0.223	r76 = 0.141, p=0.219	r89 = 0.044, p=0.678	r81 = 0.057, p=0.610	r75 = 0.014, p=0.902	r62 = -0.068, p=0.593	r59 = -0.226, p=0.080	r57 = -0.149, p=0.261	r79 = 0.017, p=0.878
P3L																			r77 = 0.097, p=0.394	r76 = 0.080, p=0.488	r83 = 0.235, p=0.030	r75 = 0.140, p=0.225	r75 = -0.089, p=0.440	r62 = -0.243, p=0.053	r59 = -0.273, p=0.033	r57 = -0.200, p=0.129	r79 = -0.004, p=0.974
P4L																				r75 = 0.425, p=0.0001	r77 = 0.045, p=0.692	r69 = 0.049, p=0.683	r74 = 0.166, p=0.152	r61 = 0.208, p=0.102	r58 = 0.049, p=0.710	r56 = 0.176, p=0.186	r77 = 0.238, p=0.034
P4W																					r76 = 0.106, p=0.358	r68 = 0.004, p=0.977	r73 = 0.298, p=0.009	r60 = 0.350, p=0.005	r57 = -0.099, p=0.453	r55 = 0.297, p=0.025	r76 = 0.289, p=0.010
M1L																						r97 = 0.772, p=0.0001	r75 = 0.151, p=0.191	r62 = 0.103, p=0.419	r59 = 0.008, p=0.949	r57 = 0.022, p=0.870	r79 = 0.223, p=0.045
M1W																							r69 = 0.024, p=0.844	r54 = 0.203, p=0.133	r51 = -0.049, p=0.730	r50 = 0.009, p=0.951	r71 = 0.187, p=0.113
M2W																								r59 = -0.039, p=0.764	r56 = 0.085, p=0.527	r54 = 0.007, p=0.960	r75 = 0.455, p=0.0001
P1P4L																									r59 = 0.126, p=0.332	r57 = 0.303, p=0.019	r62 = -0.055, p=0.664
P1M2L																										r57 = 0.129, p=0.330	r59 = 0.325, p=0.011
C1M2L																											r57 = 0.017, p=0.897
M1M2L																											

Table 5.12. Results from Pearson Correlation for the *C. lupus* dataset. Strong positive correlations indicated by $p<0.05$

m1Ltrig is more strongly positively correlated to m1W (r_{126} = 0.800, *p*= 0.0001). m1Ltal more moderately positively correlated to m1W (r_{125} = 0.409, *p* = 0.0001). m2L is strongly positively correlated with m2W (r_{105} = 0.665, *p*=0.0001) only. P4L has a moderately strong positive correlation with P4W (r_{75} = 0.425, *p*=0.0001), M1L has a strong positive correlation with M1W (r_{97} = 0.772, *p*=0.0001). Finally, M2W has a moderately strong positive correlation with M1M2L (r_{75} = 0.455, *p*=0.0001).

5.1.4. Variation in measurements

The coefficient of variation (CV) was calculated for *C. lupus* (including all Pleistocene Britain and mainland European individuals, plus the recent European *C. lupus* dataset). Table 5.13 shows the results, with the mean and standard deviation given.

Measurement	Mean	SD	CV species
p4L	16.02	0.895	5.584
p4W	8.16	0.633	7.753
m1L	29.18	1.567	5.370
m1Ltrig	20.46	1.181	5.769
m1Ltal	7.61	0.634	8.337
m1W	11.69	0.744	6.365
m2L	11.74	0.776	6.611
m2W	8.87	0.631	7.117
p1p4L	50.38	2.687	5.334
p2p4L	43.82	2.304	5.257
p1m3L	95.66	3.578	3.740
p2m3L	89.17	3.515	3.942
DentaryL	174.83	9.673	5.533
p3p4D	27.59	2.221	8.049
p3p4B	12.78	1.285	10.057
m1m2D	32.07	3.038	9.472
m1m2B	13.03	1.225	9.402
P3L	15.95	1.108	6.949
P4L	26.35	1.379	5.235
P4W	14.03	1.119	7.976
M1L	16.62	1.041	6.263
M1W	22.38	1.573	7.027
M2W	14.10	0.901	6.391
P1P4L	64.03	3.716	5.803
P1M2L	83.73	3.688	4.405
C1M2L	86.35	3.925	4.545
M1M2L	23.15	1.699	7.341

Table 5.13. Coefficients of variation (CV) for measurements of *C. lupus*, shown with mean and standard deviation. Measurement abbreviations in Chapter 4.

The above results are illustrated in Figure 5.1. The measurements with the lowest variability are p1m3L, p2m3L, P1M2L, C1M2L, p2p4L, p1p4L, followed by m1L and P4L. The measurements with the highest variability include p3p4B, m1m2D, m1m2B, p3p4D, as well

as m1Ltal, P4W p4W, M1M2L, m2W. In general, p4L is less variable than p4W. Both carnassials and the whole mandible and maxilla measurements have the lowest variability, whereas molars, and jaw depth and width are more variable.

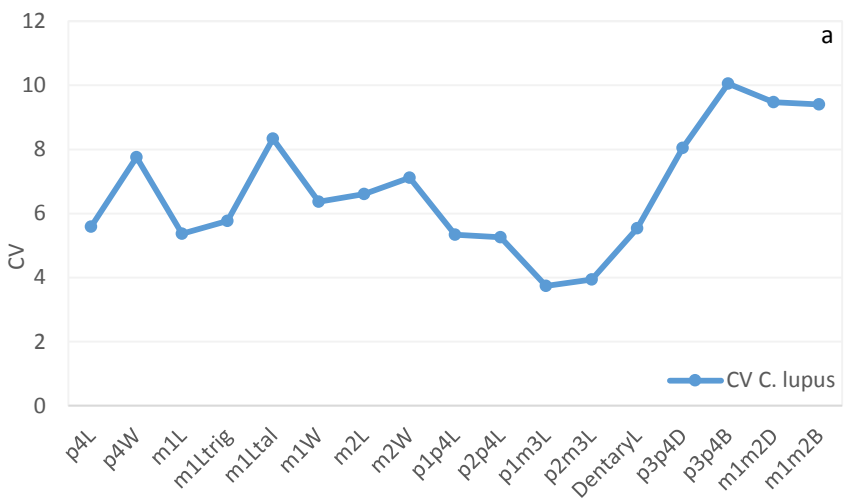
The CV was also investigated for measurements of *C. mosbachensis* (Table 5.14.).

Measurement	Mean	SD	CV species
p4L	13.69	0.950	6.938
p4W	6.28	0.640	10.180
m1L	24.11	1.169	4.846
m1Ltrig	16.24	1.020	6.286
m1Ltal	6.71	0.393	5.859
m1W	9.23	0.616	6.677
m2L	10.20	0.894	8.764
m2W	7.57	0.687	9.074
p1p4L	43.17	1.779	4.120
p2p4L	38.22	2.867	7.500
p1m3L	82.30	2.657	3.229
p2m3L	77.20	3.027	3.921
DentaryL	132.04	3.925	2.972
p3p4D	19.68	2.607	13.251
p3p4B	9.19	1.245	13.551
m1m2D	22.14	2.119	9.571
m1m2B	10.01	0.835	8.340
P3L	13.55	0.826	6.095
P4L	22.57	1.161	5.145
P4W	11.00	0.796	7.241
M1L	13.60	0.724	5.325
M1W	18.66	1.147	6.148
M2L	7.62	0.887	11.648
M2W	12.13	1.092	9.001
P1P4L	57.99	2.658	4.584
P1M2L	75.85	2.284	3.011
C1M2L	77.36	3.107	4.017
M1M2L	19.76	1.253	6.342

Table 5.14. Coefficients of variation (CV) for measurements of *C. mosbachensis* shown with mean and standard deviation. Measurement abbreviations in Chapter 4.

The above results are illustrated in Figure 5.2. The measurements with the lowest variation are DentaryL, P1M2L, p1m3L, p2m3L, C1M2L, followed by m1L and P4L. The most highly variable measurements are p3p4B, p3p4B, M2L, p4W.

As with *C. lupus*, p4L is less variable than p4W. Both carnassials and whole mandibular and maxillary measurements have lowest variability, whereas molars, and jaw depth and width are more variable. Comparison of Figure 5.1 and 5.2, for *C. lupus* and *C. mosbachensis* respectively, reveals that the variability between each species measurements is similar, albeit the highest values of CV in *C. mosbachensis* are higher than in *C. lupus*.



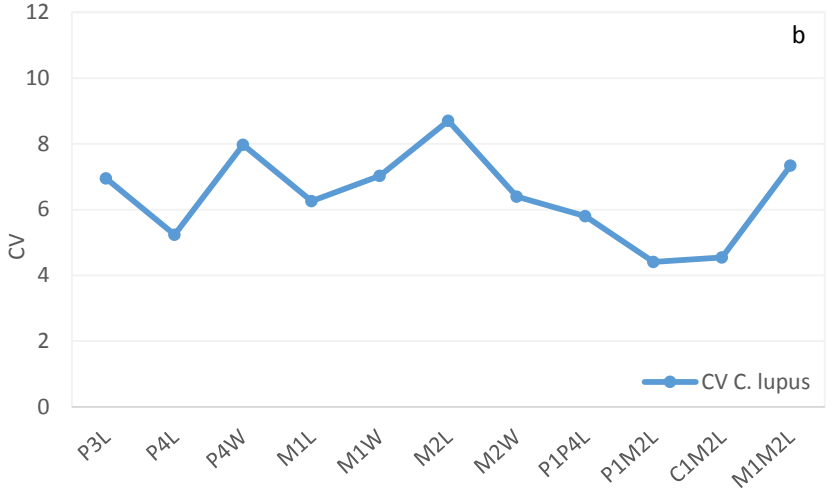
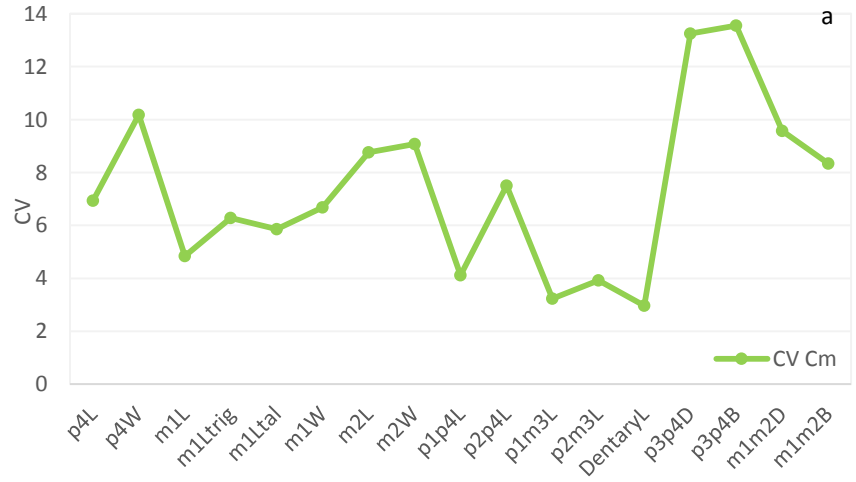


Figure 5.1. Coefficients of variation (CV) for measurements of *C. lupus*: a). mandible and lower teeth. b). maxilla and upper teeth.



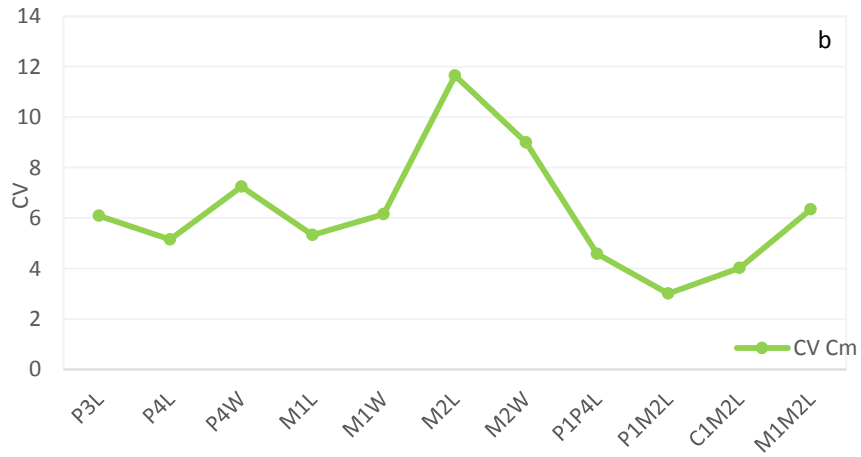


Figure 5.2. Coefficients of variation (CV) for measurements of *C. mosbachensis*: a) mandible and lower teeth, b) maxilla and upper teeth.

The CV was also investigated for measurements of *C. arnensis* (Table 5.15.) although low numbers of individuals for certain measurements may have influenced CV for P1P4L, P1M3L, C1M2L. There were no individuals available for DentaryL measurement.

Measurement	Mean	SD	CV species
p4L	13.22	0.484	3.660
p4W	5.84	0.249	4.266
m1L	21.93	1.056	4.818
m1Ltrig	14.64	0.635	4.337
m1Ltal	6.29	0.453	7.196
m1W	8.36	0.396	4.739
m2L	10.15	0.663	6.538
m2W	7.08	0.535	7.557
p1p4L	43.90	1.688	3.846
p2p4L	37.90	1.775	4.683
p1m3L	79.59	3.189	4.006
p2m3L	73.87	3.396	4.598
DentaryL	N/A		
p3p4D	18.37	2.051	11.165
p3p4B	7.99	0.144	1.797
m1m2D	21.34	1.900	8.903
m1m2B	9.09	0.970	10.677
P3L	12.17	0.500	4.105
P4L	20.17	0.309	1.531
P4W	9.61	0.703	7.315
M1L	13.10	0.862	6.581
M1W	17.74	0.924	5.209
M2L	6.89	0.260	3.777
M2W	11.51	0.579	5.031
P1P4L	54.39	0.106	0.195
P1M2L	70.88	0.580	0.819
C1M2L	73.09	2.370	3.243
M1M2L	18.23	0.269	1.477

Table 5.15. Coefficients of variation (CV) for measurements of *C. arnensis* shown with mean and standard deviation. Measurements abbreviations in Chapter 4.

The results shown in Table 5.5 are illustrated in Figure 5.3. The measurements with the lowest variability include p3p4B, M1M2L, P4L, M2L, P4L, p1p4L, m1L. The measurements with the highest amounts of variability include p3p4D, m1m2D, m1Ltal, m2W and P4W.

In general, and broadly similar to both *C. lupus* and *C. mosbachensis*, p4L is less variable than p4W. The carnassials are less variable in comparison to the molars, which have high variability. Jaw depth and width are both highly variable, although (where available), whole mandible and maxilla lengths have lower variability. The variation present in *C. arnensis*, however, may relate to low sample numbers.

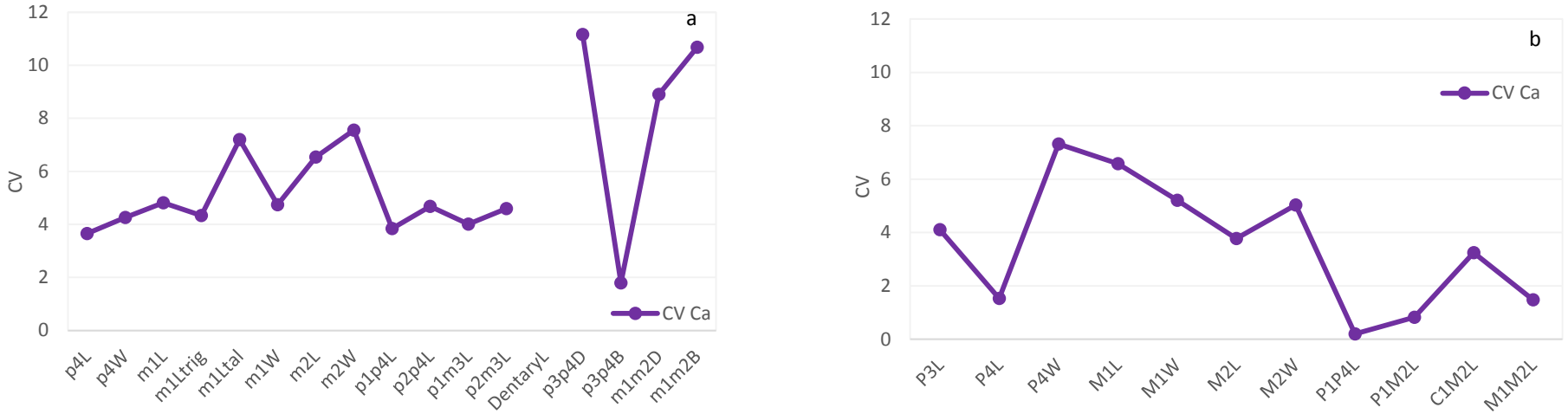


Figure 5.3. Coefficients of variation (CV) for measurements of *C. arnensis*: a) mandible and lower teeth, b) maxilla and upper teeth.

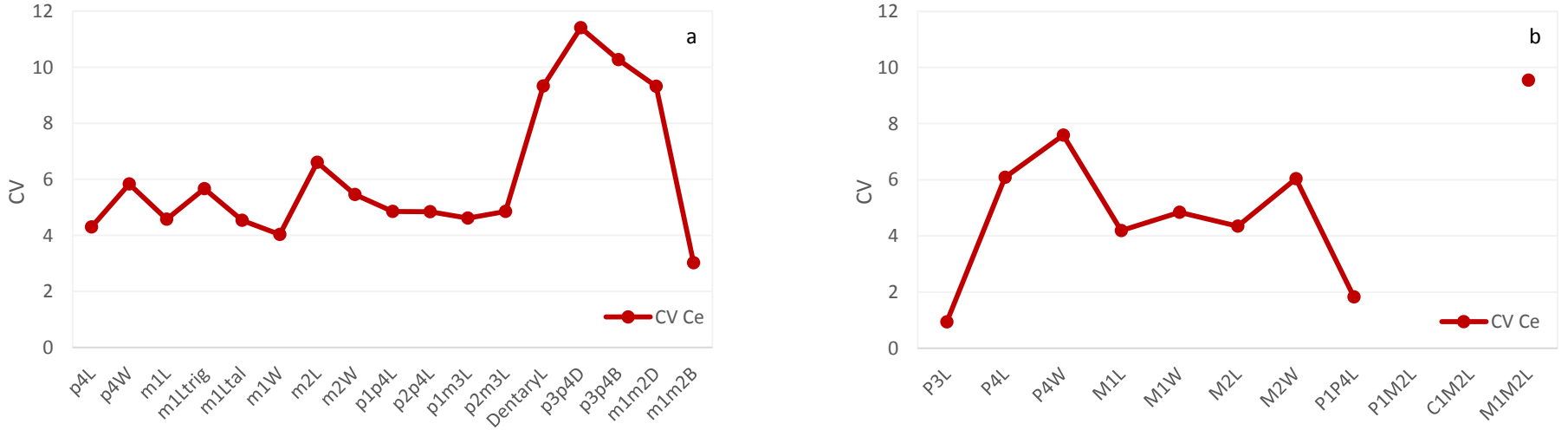


Figure 5.4. Coefficients of variation (CV) for measurements of *C. etruscus*: a) mandible and lower teeth, b) maxilla and upper teeth.

The CV was also investigated for measurements of *C. etruscus* (Table 5.16.). However, low numbers of individuals for certain measurements may cause inflation of CV for DentaryL and P1P4L. No individuals were present in P1M3L and C1M2L measurements.

Measurement	Mean	SD	CV species
p4L	15.12	0.651	4.306
p4W	6.88	0.401	5.835
m1L	25.05	1.147	4.576
m1Ltrig	16.94	0.960	5.666
m1Ltal	6.89	0.312	4.535
m1W	9.642	0.389	4.030
m2L	11.04	0.729	6.606
m2W	7.87	0.429	5.456
p1p4L	48.30	2.346	4.856
p2p4L	41.22	1.997	4.844
p1m3L	88.67	4.098	4.621
p2m3L	82.41	4.002	4.856
DentaryL	142.28	13.277	9.332
p3p4D	21.35	2.436	11.409
p3p4B	9.88	1.014	10.267
m1m2D	24.56	2.288	9.316
m1m2B	10.61	0.321	3.024
P3L	14.26	0.134	0.943
P4L	22.29	1.356	6.083
P4W	11.42	0.867	7.587
M1L	15.56	0.652	4.189
M1W	20.33	0.985	4.845
M2L	7.77	0.338	4.349
M2W	12.35	0.745	6.033
P1P4L	59.80	1.096	1.833
P1M2L	N/A		
C1M2L	N/A		
M1M2L	21.67	2.069	9.548

Table 5.16. Coefficients of variation (CV) for measurements of *C. etruscus* shown with mean and standard deviation. N/A no measurement possible. Measurement abbreviations in Chapter 4.

The results shown in Table 5.16 are illustrated by Figure 5.4. The measurements with the lowest variability include P3L, m1m2B, m1W, M1L, m1L. The measurements with the highest variability include p3p4D, p3p4B, m1m2D, m2L, P4W.

In general, and broadly similar to the aforementioned three taxa, p4L is less variable than p4W in *C. arnensis*. The carnassials are less variable in comparison to the molars, which display high variability. Jaw depth and width are both highly variable, whereas (where available), whole mandible and maxilla lengths have lower variability. However, like *C. arnensis*, the variation present may also relate to low sample numbers.

5.1.5. Temporal and regional comparisons of measurement data

This section shows the analysed dietary measurements grouped by site, both as individual measurements and mean values for an age group. Graphical comparisons between sites, age groups and species for Britain and Europe are shown.

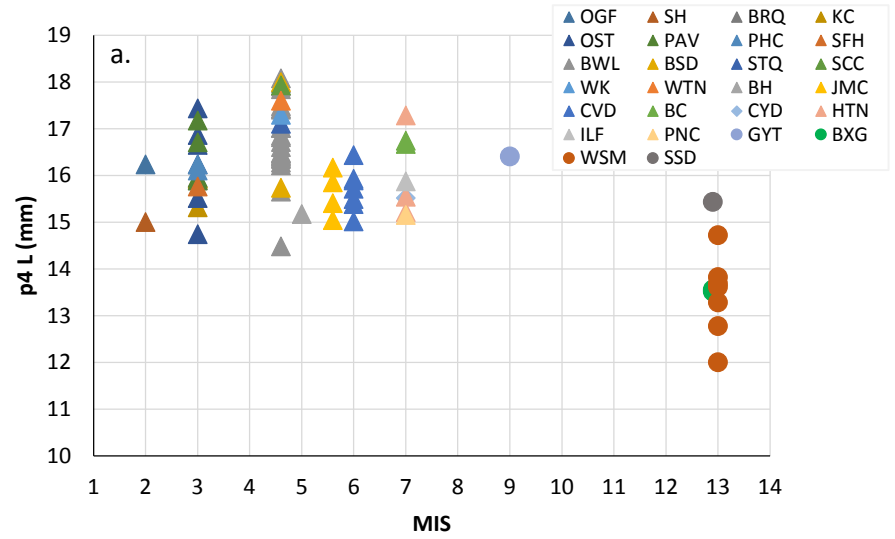
5.1.5.1. Lower fourth premolar (p4)

Figures 5.5 and 5.6 compare p4L, and Figures 5.7 and 5.8 compare p4W in sites and between age groups in Britain and mainland Europe. Within-age group and within-site variation is high. Both p4L and p4W are larger in *C. lupus* than in *C. mosbachensis* and *C. arnensis* with some overlap present with *C. etruscus*. *C. arnensis* is similar to *C. mosbachensis* in p4L, yet has narrower p4W. *C. etruscus* has larger p4L and p4W than *C. arnensis*. In Britain (Figure 5.5b, 5.7b), mean p4L and p4W for MIS 5a *C. lupus* contains the largest values, with MIS 2, 3, 5c, 5e, 6 and 7 more similar. The mainland European Late Pleistocene broad age groups are also similar in p4L and p4W. Comparison of Figures 5.5 and 5.6 for p4L and 5.7 and 5.8 for p4W) reveals similarities Britain and Europe for *C. lupus* and *C. mosbachensis* for both measurements.

5.1.5.2. Lower carnassial (m1)

Figures 5.9 and 5.10 compare m1L in sites and between age groups in Britain and mainland Europe. Large individual variation is present within sites and between age groups. *C. lupus* has longer m1L than *C. mosbachensis* and *C. arnensis*, with slight overlap with *C. etruscus. C. mosbachensis* and *C. arnensis* overlap. MIS 5a *C. lupus* has the longest m1L and highest within-age group variation, with other MIS groups more similar. In Europe (Figure 5.10), late Middle Pleistocene wolves (age group 3) have shorter m1L compared to the Late Pleistocene groups. High variation is also present in *C. mosbachensis* of the Middle Pleistocene (age group 3.4) but comparison of Figures 5.9 and 5.10 reveals broad similarities between *C. lupus* and *C. mosbachensis* in Britain and mainland Europe.

Figures 5.11 and 5.12 compare m1Ltrig, in sites and between age groups in Britain and mainland Europe. Similar to m1L, high variation is present within sites and between age groups. *C. lupus* has longer m1Ltrig than *C. mosbachensis* and *C. arnensis*, with slight overlap with *C. etruscus.*



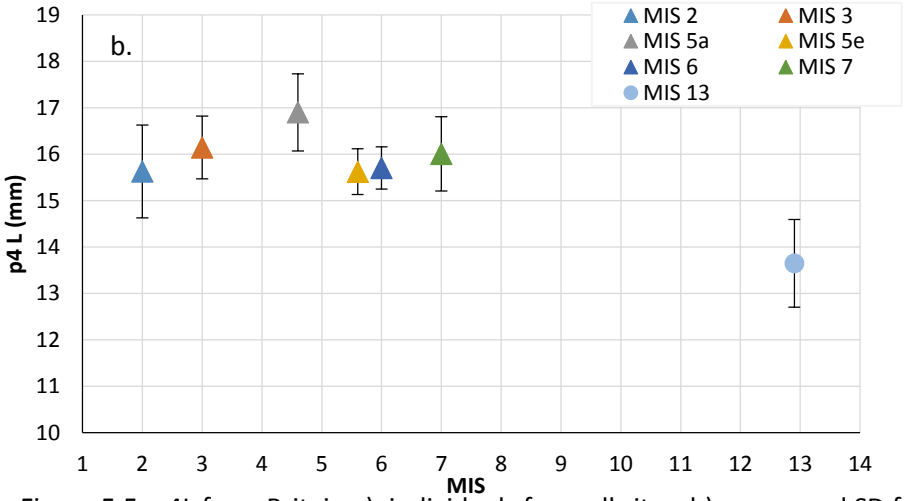
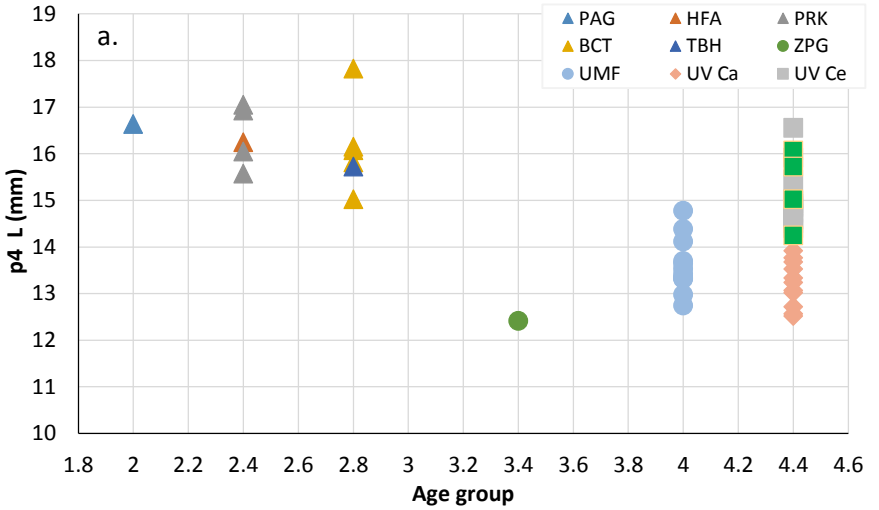


Figure 5.5. p4L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.



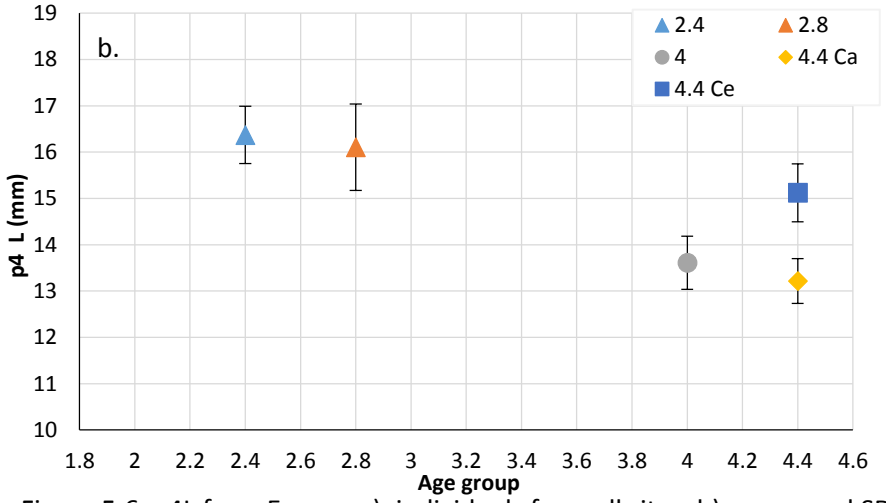
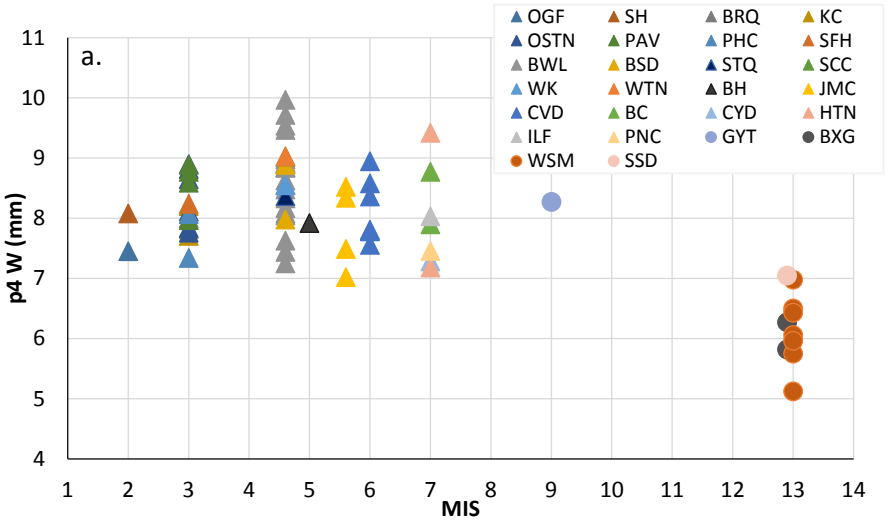


Figure 5.6. p4L from Europe a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊



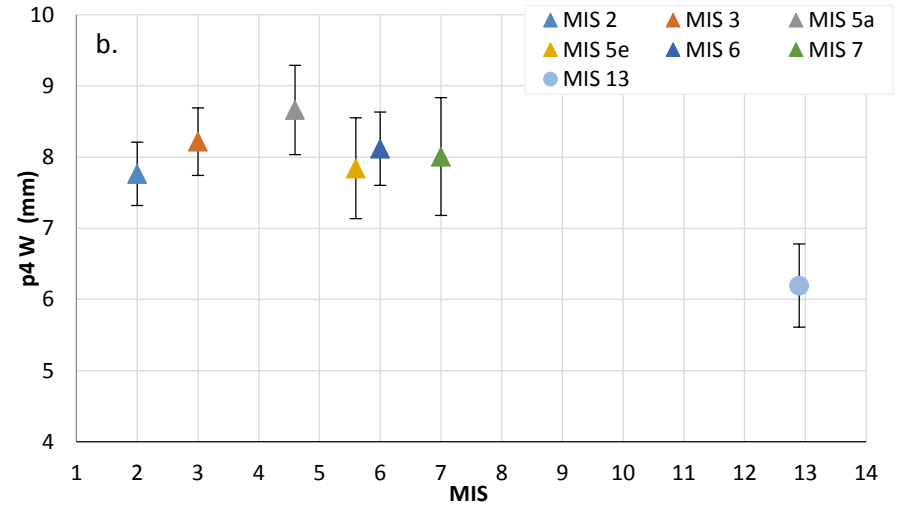
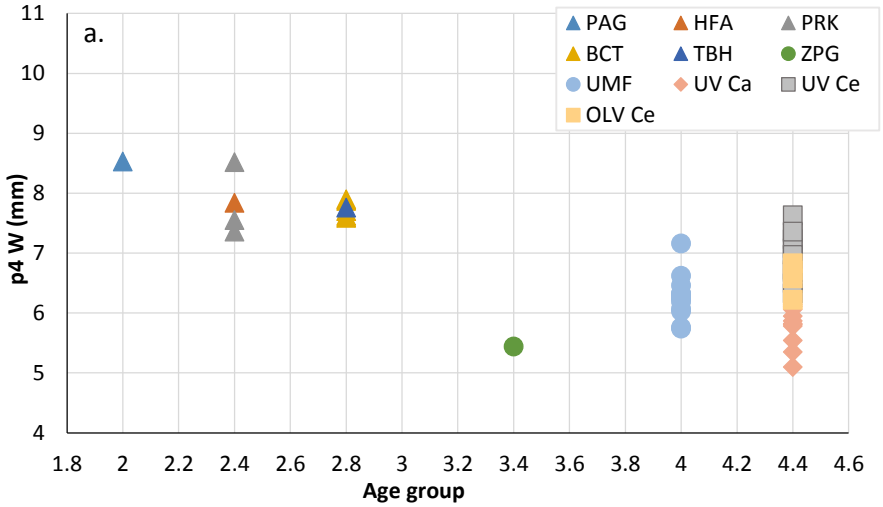


Figure 5.7. p4W from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.



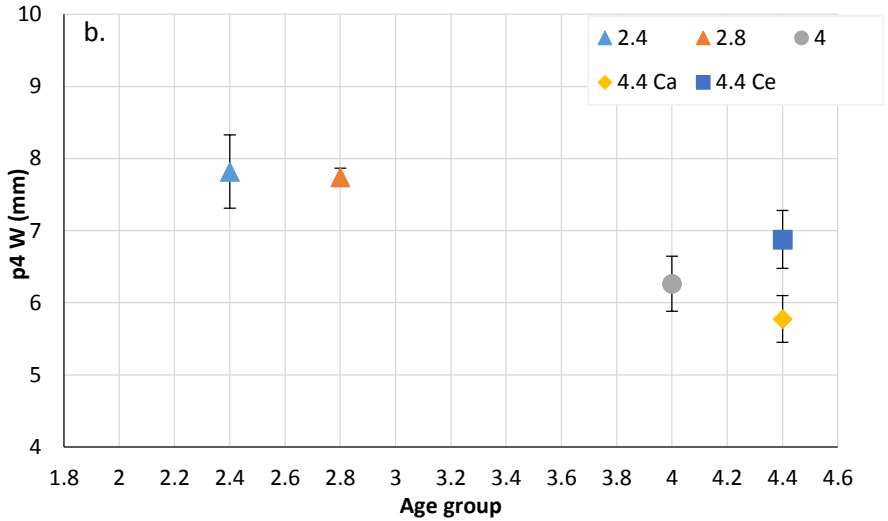
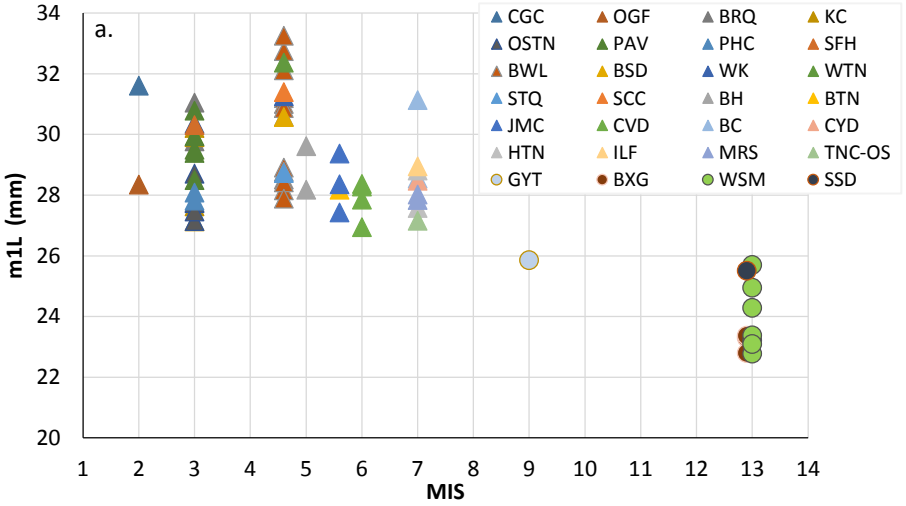


Figure 5.8. p4W from Europe a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊



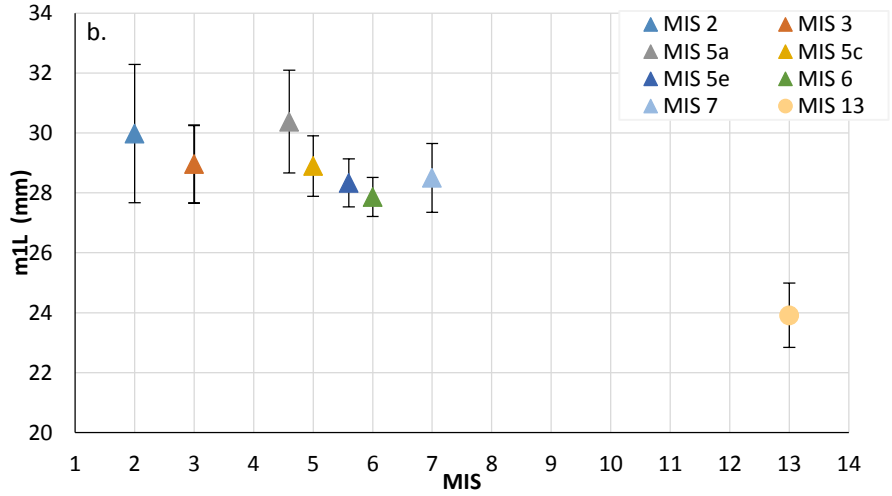
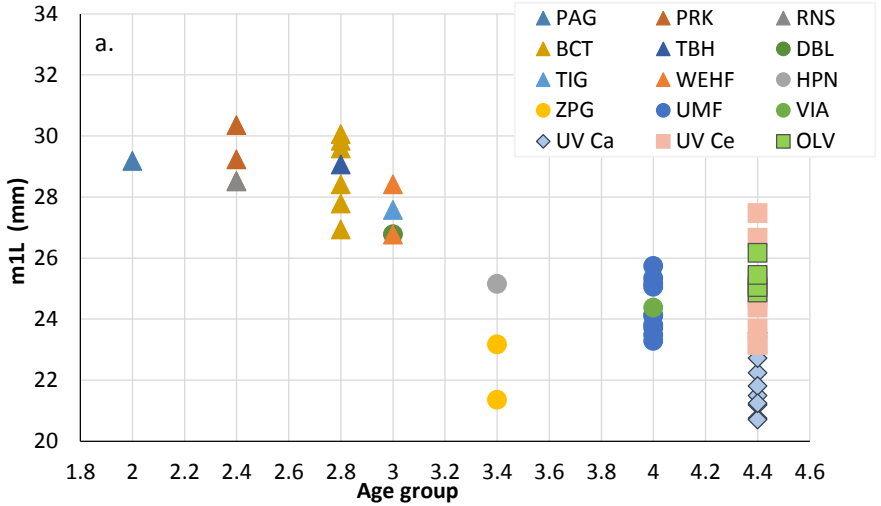


Figure 5.9. m1L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.



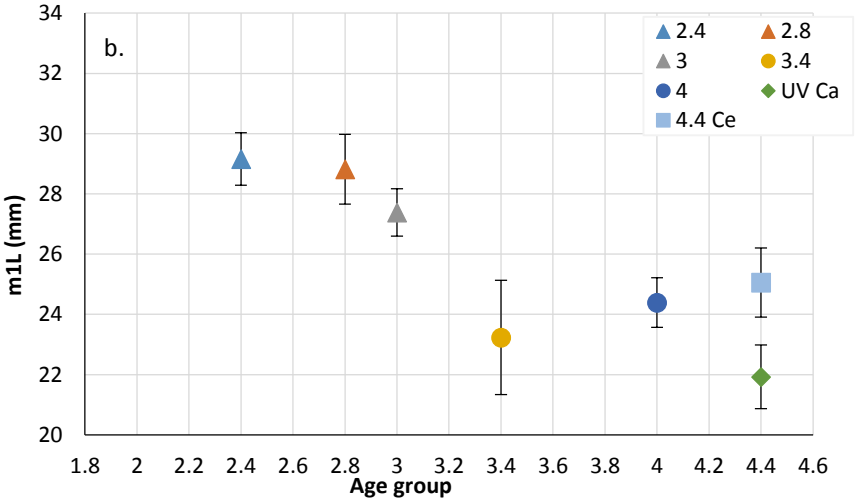


Figure 5.10. m1L from mainland Europe a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

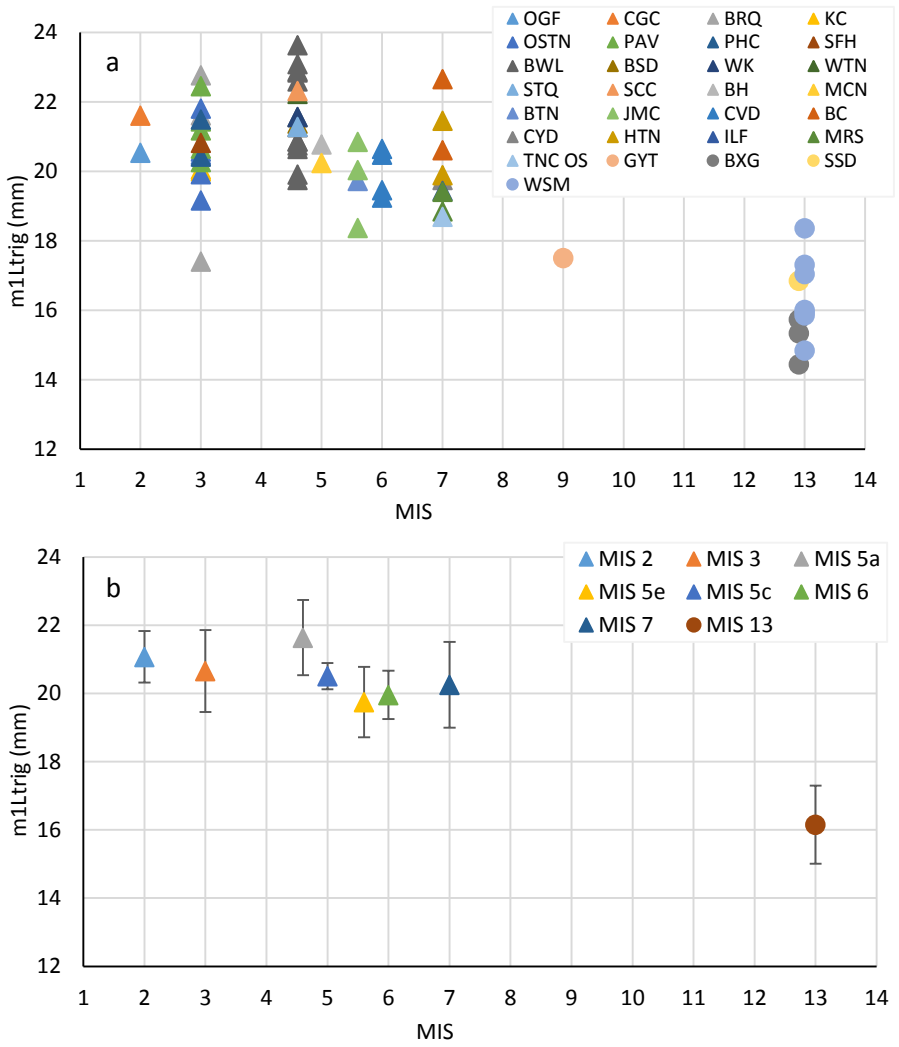


Figure 5.11. m1Ltrig from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

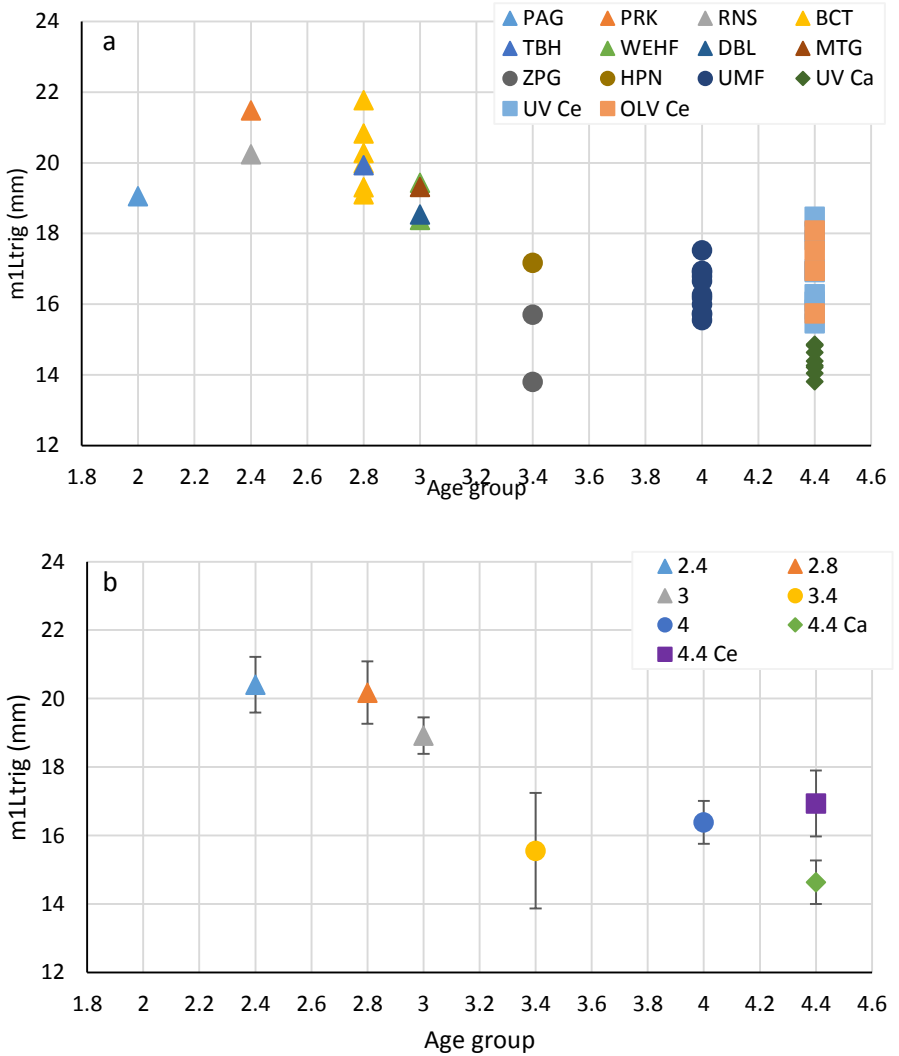


Figure 5.12. m1Ltrig from Europe a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

C. mosbachensis and *C. arnensis* overlap in the Middle Pleistocene age group (3.4). MIS 5a *C. lupus* contains the longest m1Ltrig, with high within-age group variation noted also for MIS 3 and 7. In Europe (Figure 5.12), late Middle Pleistocene (age group 3) wolves had shorter m1Ltrig. Figures 5.9 and 5.10 indicate that *C. lupus* and *C. mosbachensis* in Britain and mainland Europe are broadly similar.

Figures 5.13 and 5.14 compare m1Ltal. m1Ltal were similar between *C. lupus* with less variation than in m1L and m1Ltrig. All species overlap in m1Ltal, unlike in other measurements on the lower carnassial.

Figures 5.15 and 5.16 compare m1W in sites and between age groups in Britain and mainland Europe. Individual variation within sites and between age groups is present. m1W shows more differentiation between the species, similar to m1L and m1Ltrig, with *C. lupus* having wider m1W than *C. mosbachensis* and *C. arnensis*. *C. etruscus* is more similar to *C. mosbachensis*, with *C. arnensis* more similar to European Middle Pleistocene *C. mosbachensis* than at any other time. In Europe (Figure 5.16) Late Middle Pleistocene (age group 3) *C. lupus* has narrower m1W than during the Late Pleistocene. Comparison of Figures 5.15 and 5.16 shows that *C. lupus* and *C. mosbachensis* are similar in both Britain and Europe.

5.1.5.3. Lower second molar (m2)

Figures 5.17 and 5.18 compare m2L, and Figures 5.19 and 5.20 compare m2W in sites and between age groups in Britain and mainland Europe. Within-site and between age groups variation is high for both measurements, with MIS 7 containing some of the shortest and narrowest m2. *C. lupus* and *C. mosbachensis* overlap in all age groups in m2L except MIS 17 (West Runton), which is of generally smaller size. More differentiation is present in m2W. Mean measurement values are similar in all age groups of *C. lupus*, with more variation in Europe between the late Early Pleistocene (age group 4) and Middle Pleistocene (age group 3.4) and *C. mosbachensis*. *C. lupus* and *C. mosbachensis* respectively appear similar between Britain and Europe.

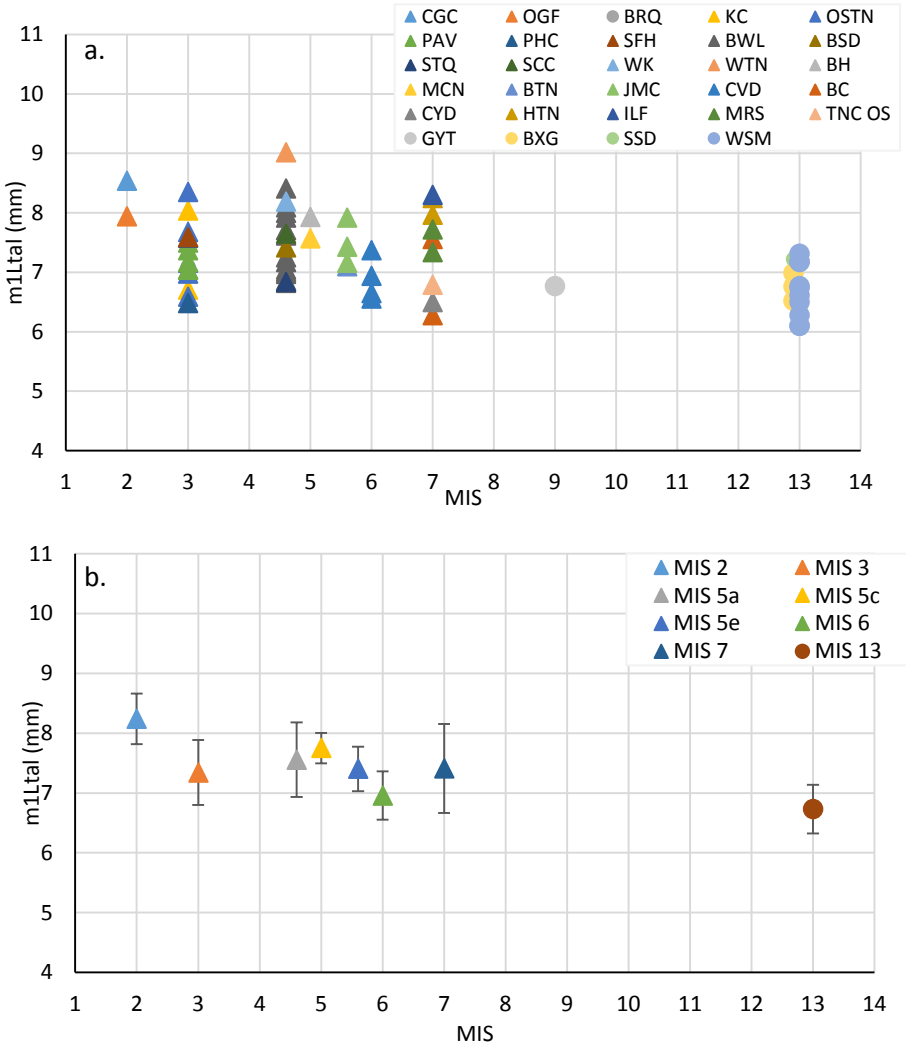


Figure 5.13. m1Ltal from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○

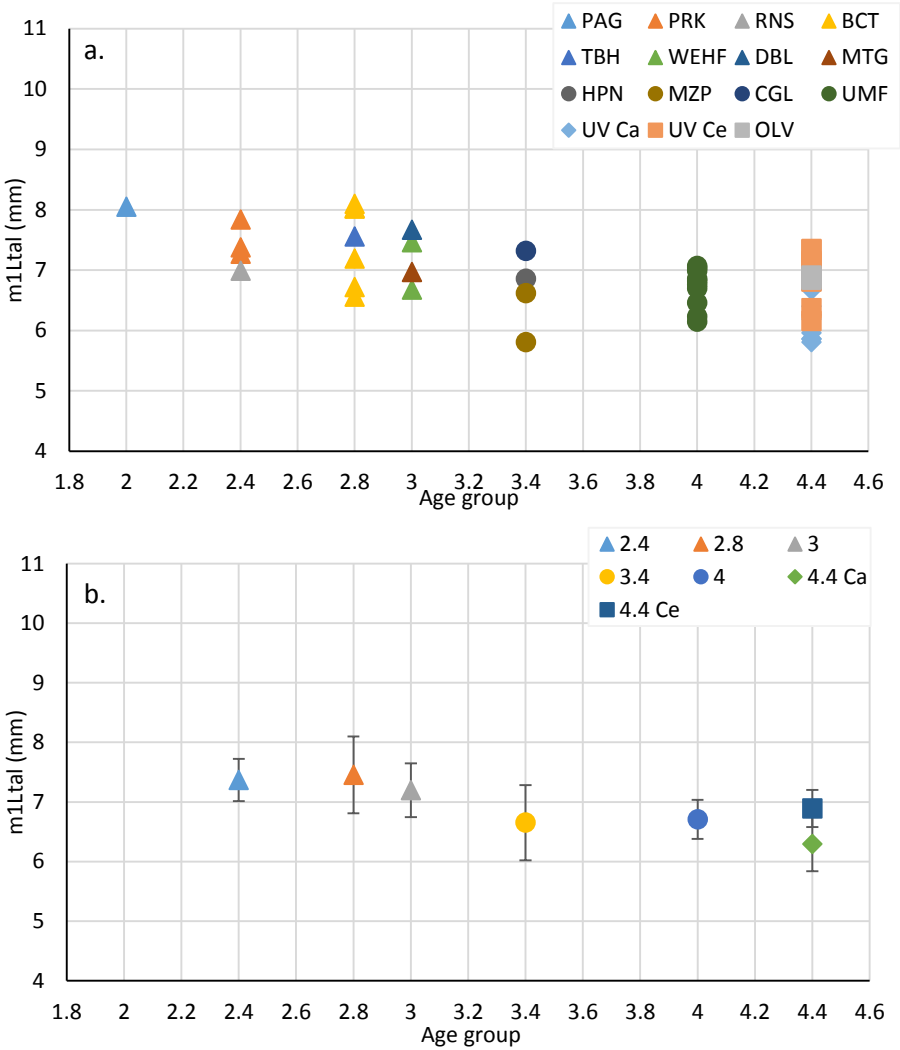


Figure 5.14. m1Ltal from Europe a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

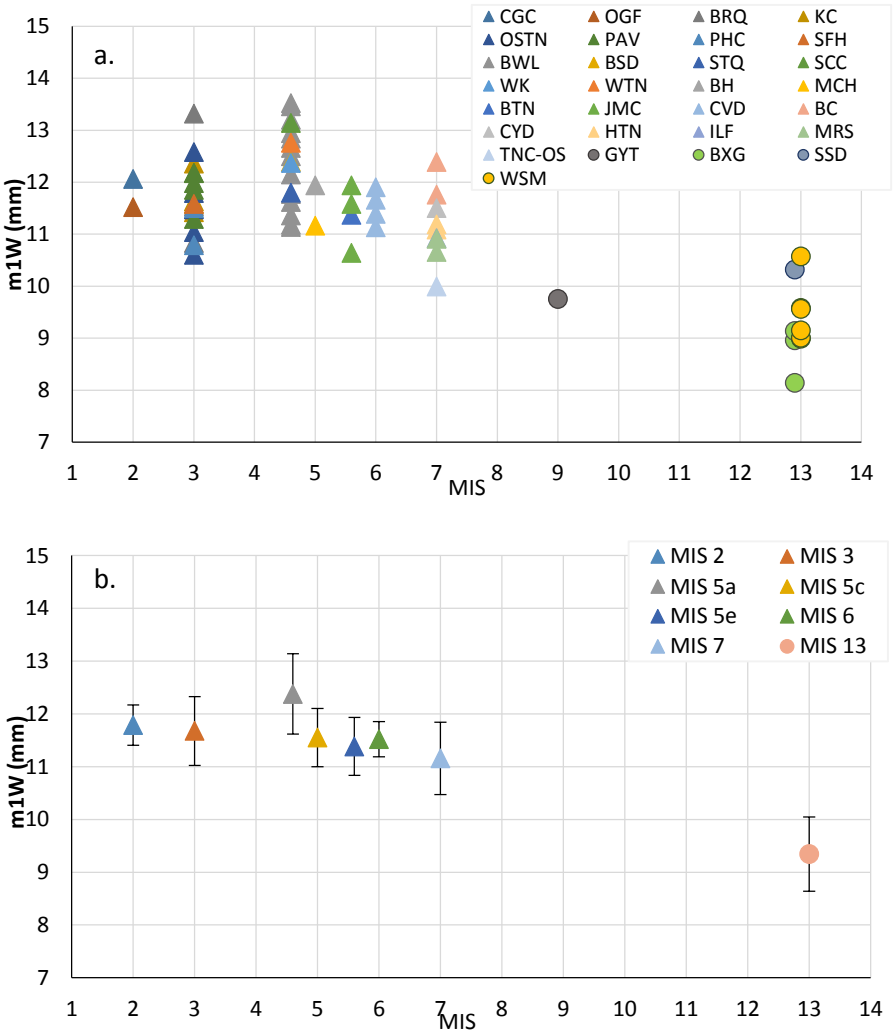


Figure 5.15. m1W from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

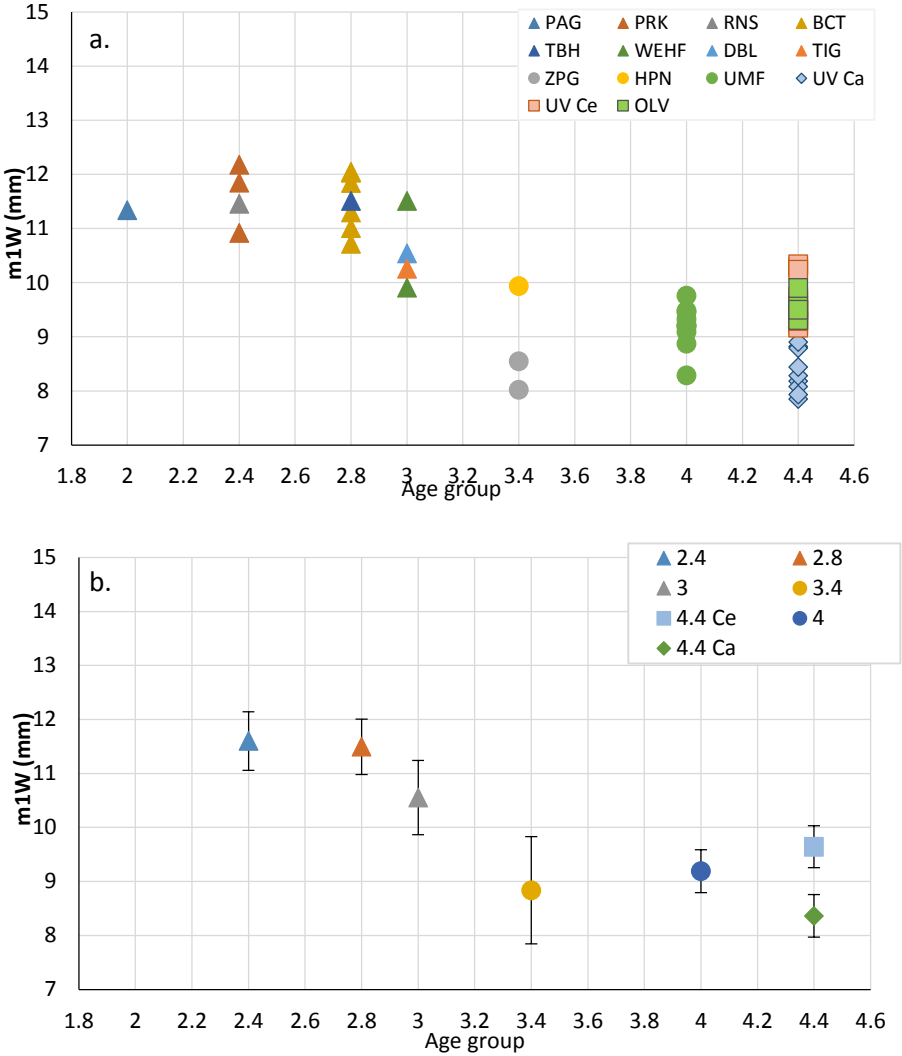


Figure 5.16. m1W from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

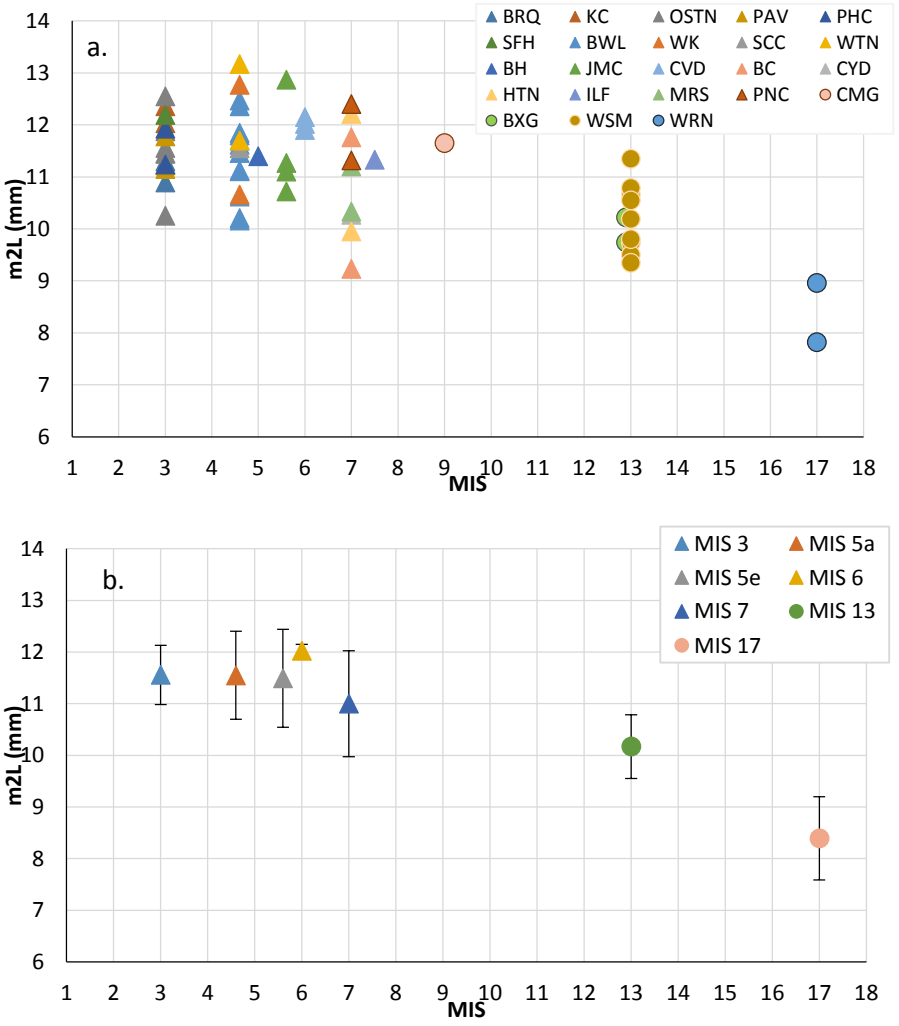


Figure 5.17. m2L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

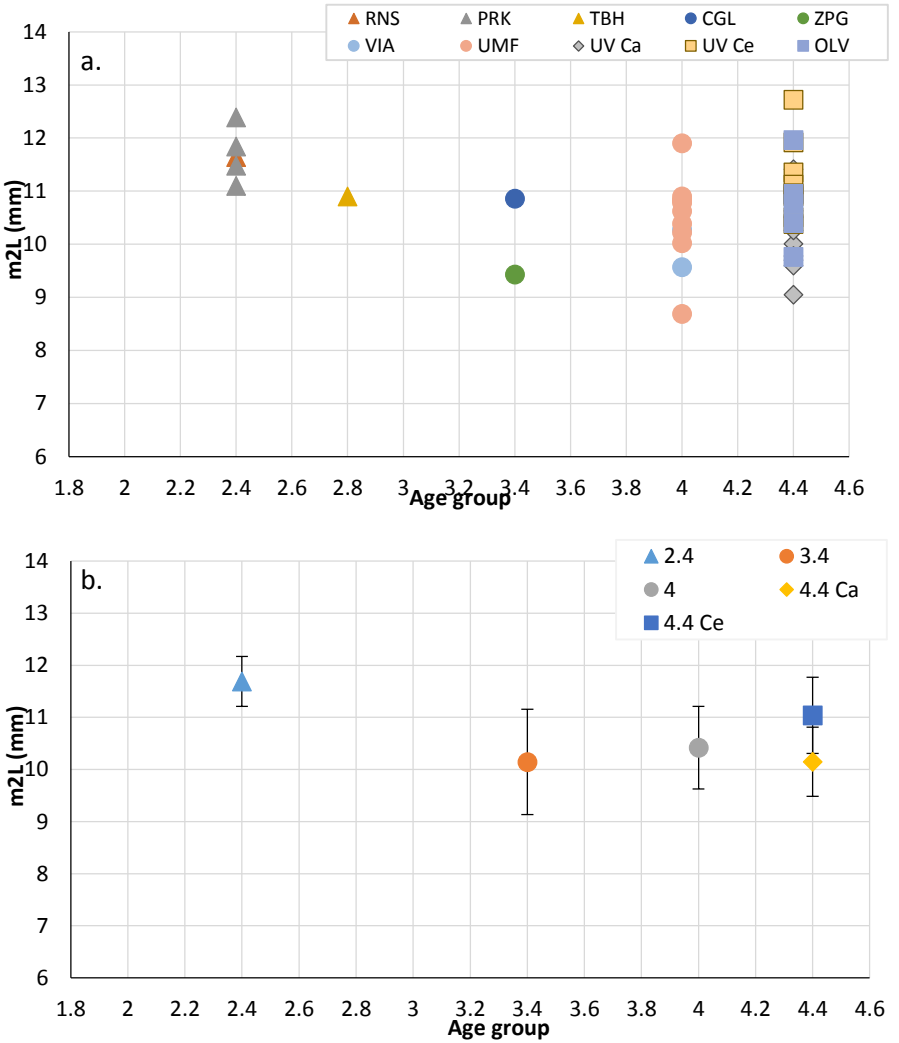


Figure 5.18. m2L from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

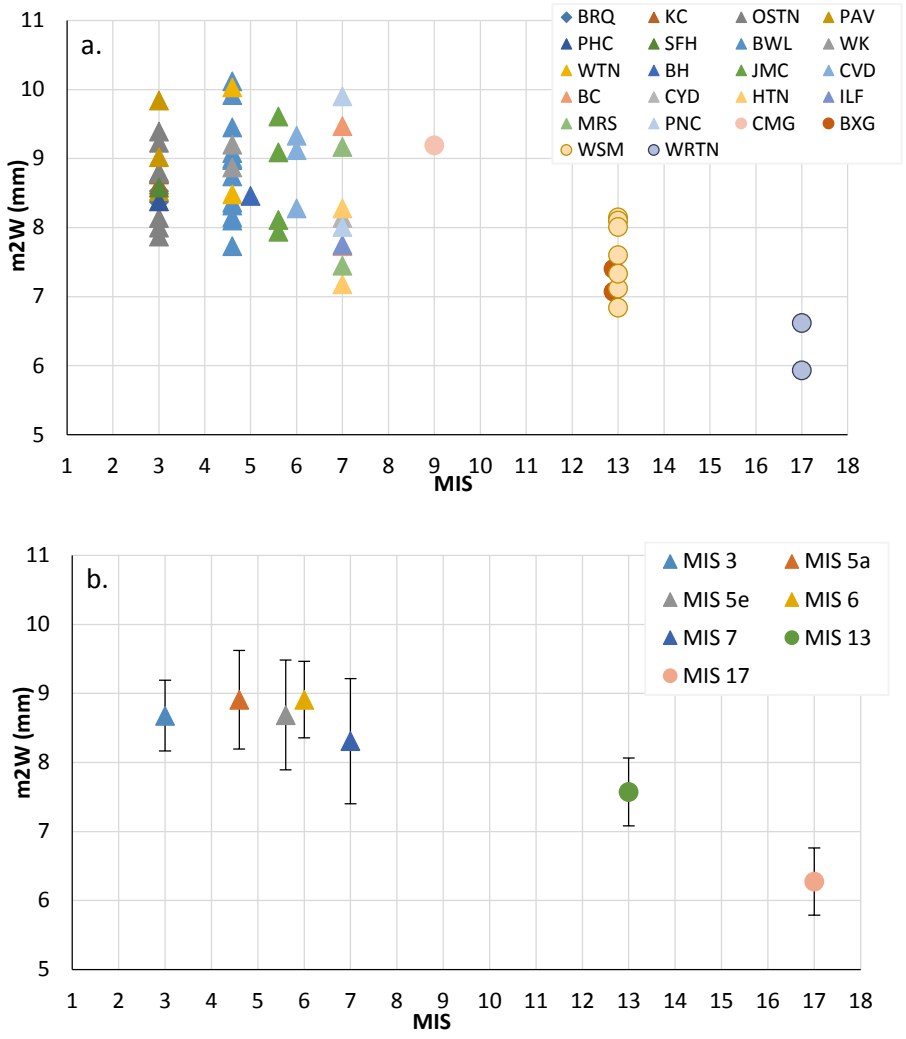


Figure 5.19. m2W from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

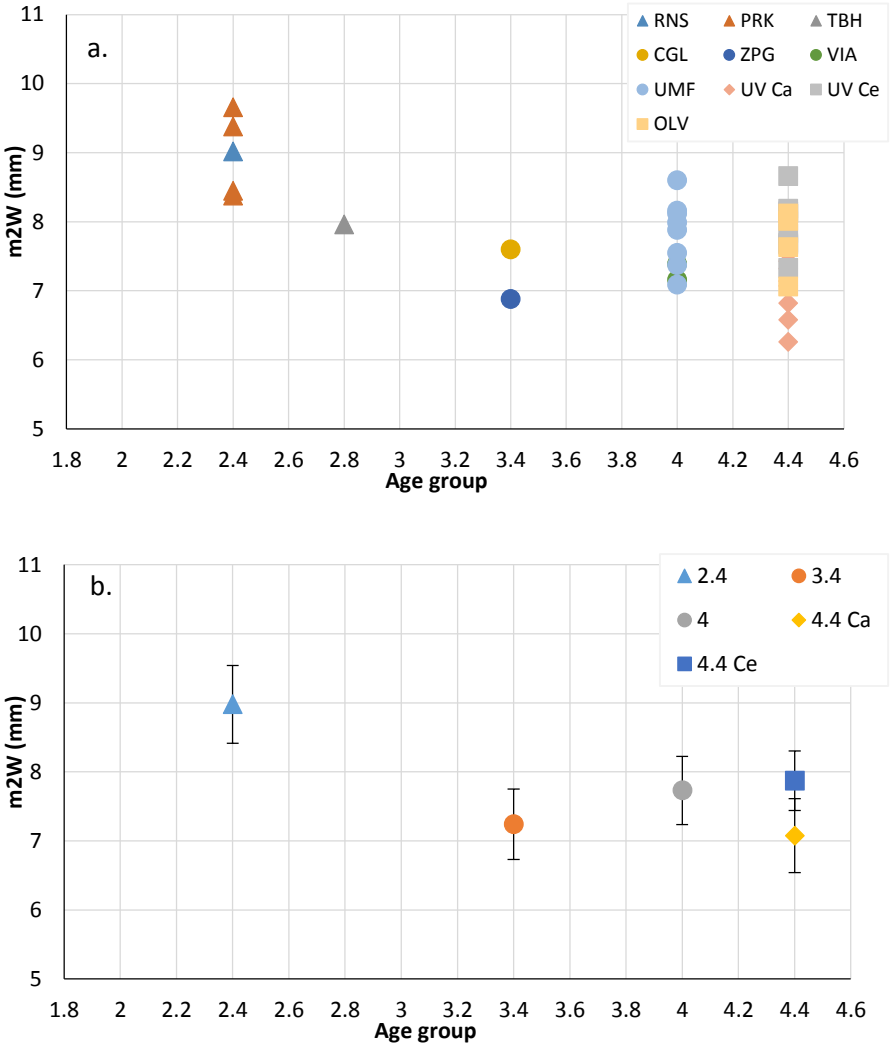


Figure 5.20. m2W from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

5.1.5.4. Lower premolar row length (p1p4L and p2p4L)

Figures 5.21 and 5.22 compare p1p4L, and Figures 5.23 and 5.24 compare p2p4L in sites and between age groups in Britain and mainland Europe. Variation is present within age groups, with *C. lupus* having longer p1p4L and p2p4L than *C. mosbachensis* and *C. arnensis*, and overlapping with *C. etruscus*. *C. mosbachensis* and *C. arnensis* are similar. In Britain, between *C. lupus*, MIS 6 has the shortest lengths. Late Pleistocene *C. lupus* from Europe is similar in both measurements. *C. lupus* and *C. mosbachensis* appear similar between Britain and Europe.

5.1.5.5. Lower cheek tooth row length (p1m3L and p2m3L)

Figures 5.25 and 5.26 compare p1m3L, and Figures 5.27 and 5.28 compare p2m3L across sites and between age groups in Britain and mainland Europe. Variation is present in both measurements for *C. lupus*, especially in Britain. Generally *C. lupus* has a longer cheek tooth row than *C. mosbachensis*, *C. arnensis* and *C. etruscus*. *C. etruscus* has a longer row than *C. mosbachensis* and *C. arnensis*, with the last two species being more similar. *C. lupus* from the late Middle Pleistocene in Britain has a slightly shorter cheek tooth row length than in the Late Pleistocene. *C. lupus* and *C. mosbachensis* compare well between Britain and Europe.

5.1.5.6. Jaw depth and breadth at the p3-p4 junction (p3p4B and p3p4D)

Figures 5.29 and 5.30 compare p3p4D, and Figures 5.31 and 5.32 compare p3p4B between sites and age groups in Britain and mainland Europe. Variation is apparent for both measurements in all species, especially in p3p4B. *C. lupus* generally has broader and deeper jaws (at p3-p4) than the other species, which all overlap. European *C. lupus* from the early Late Pleistocene (age group 2.8) contains the highest variation. MIS 7 *C. lupus* in Britain also has slightly narrower jaws compared to the Late Pleistocene. *C. lupus* and *C. mosbachensis* respectively compare well with their regional counterparts.

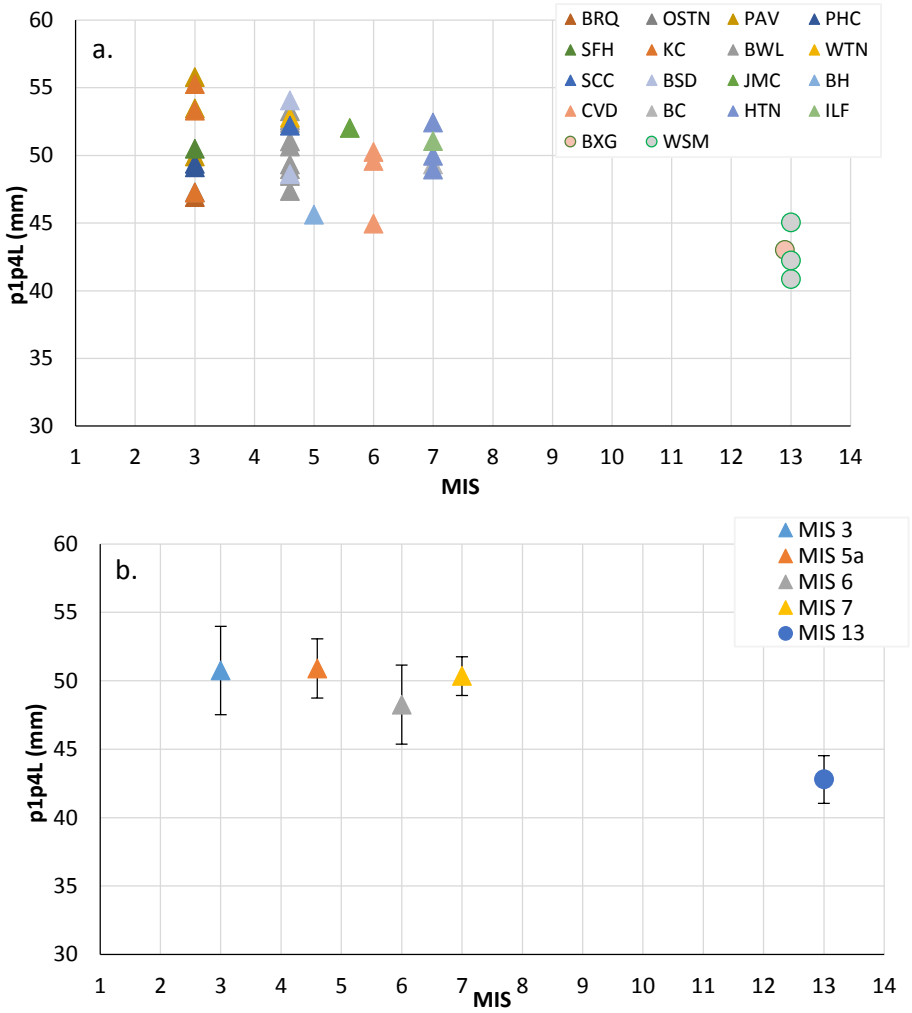


Figure 5.21. p1p4L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

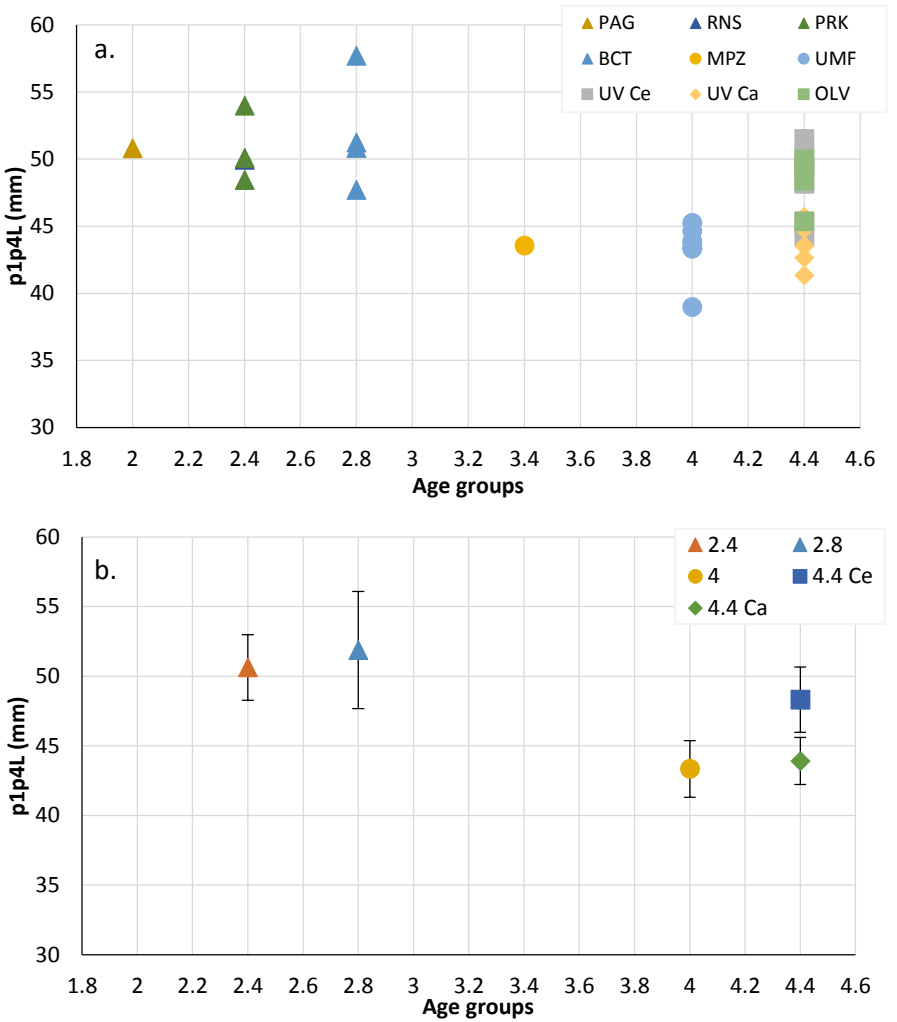
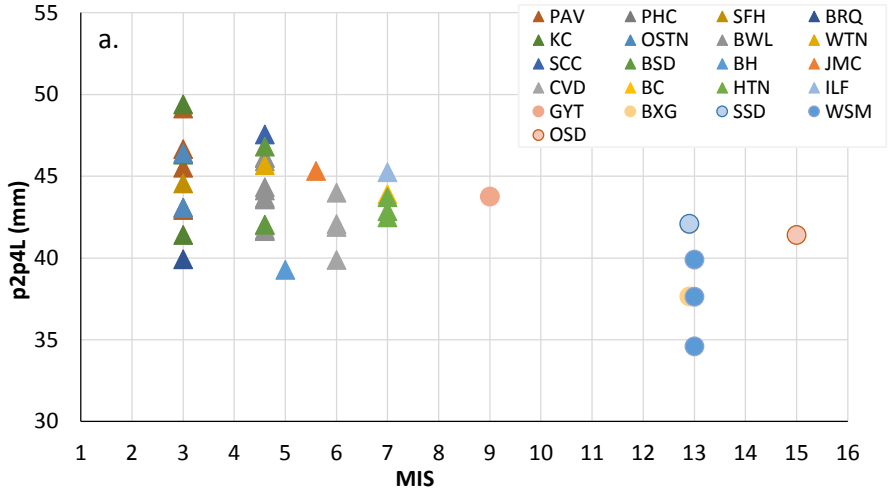


Figure 5.22. p1p4L from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊



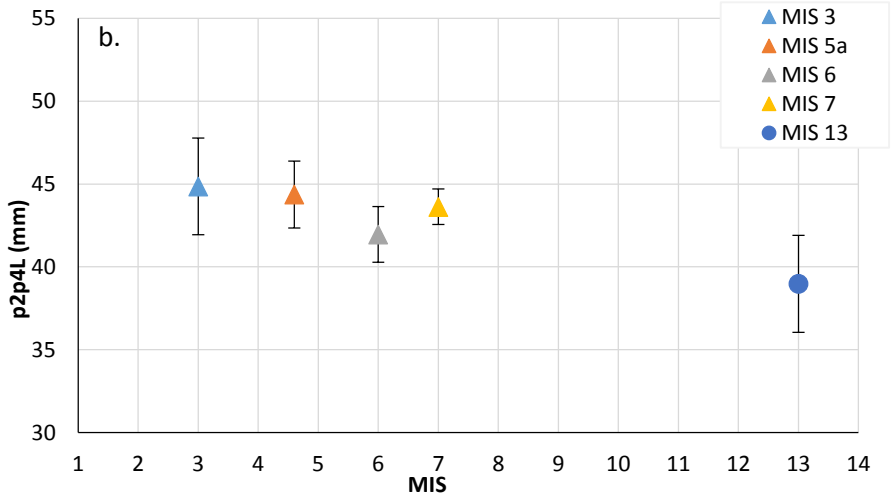
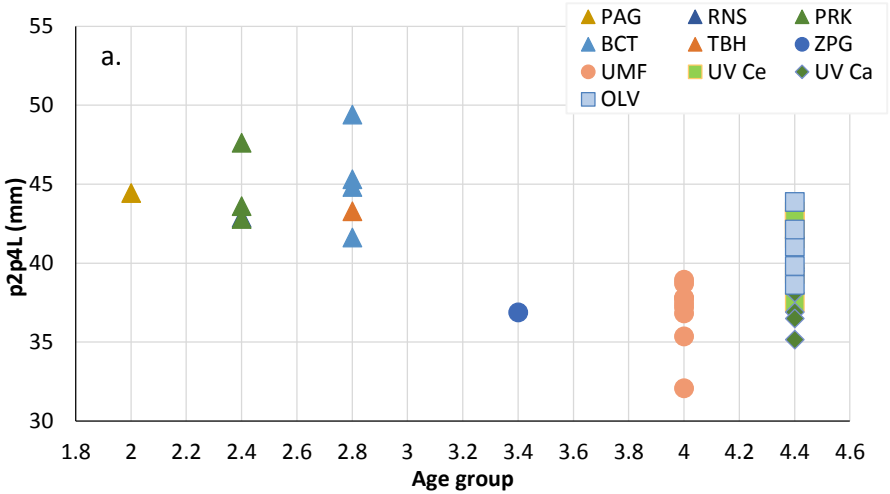


Figure 5.23. p2p4L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.



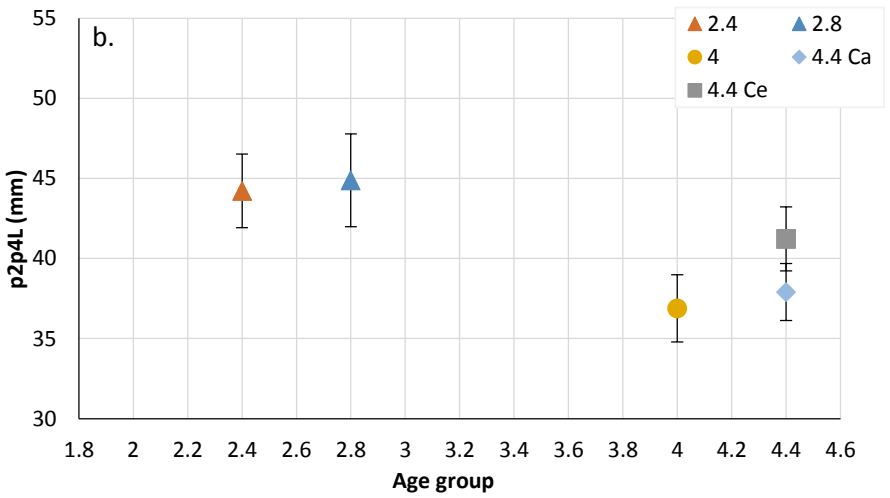
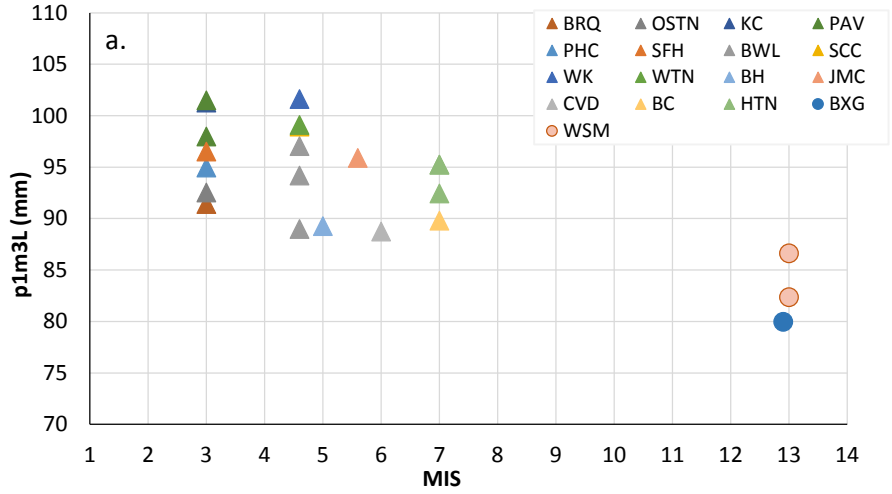


Figure 5.24. p2p4L from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊



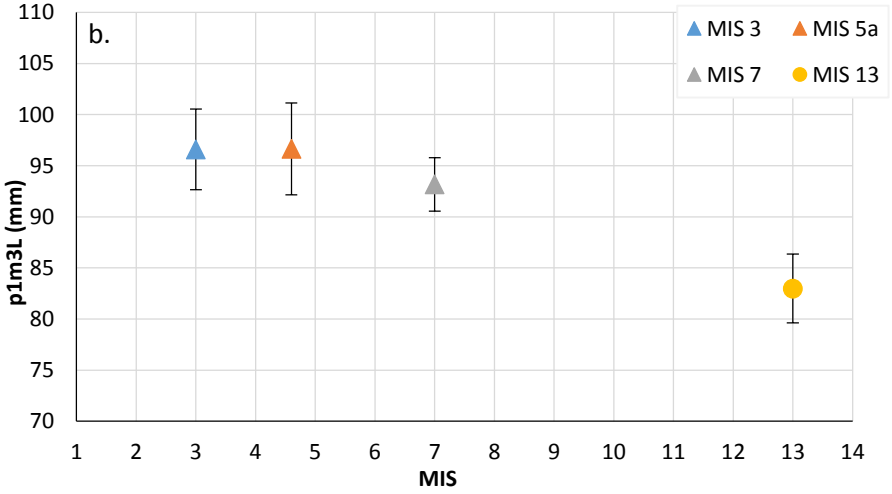
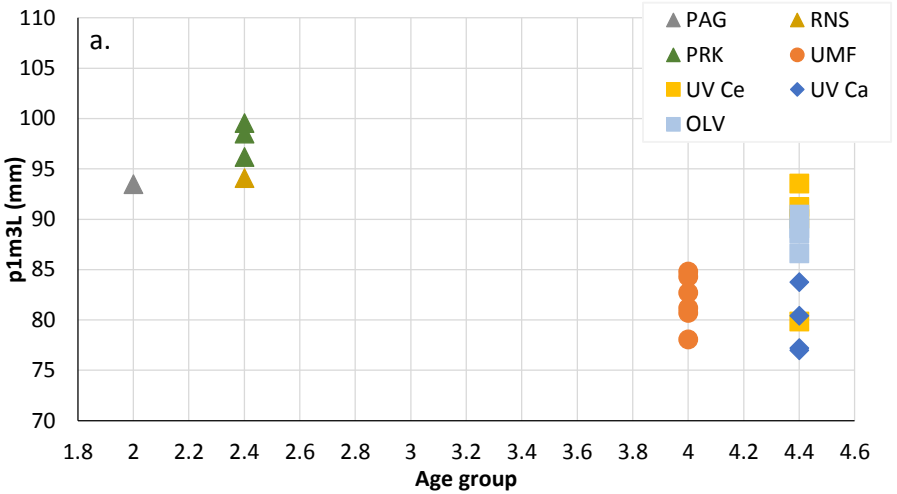


Figure 5.25. p1m3L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.



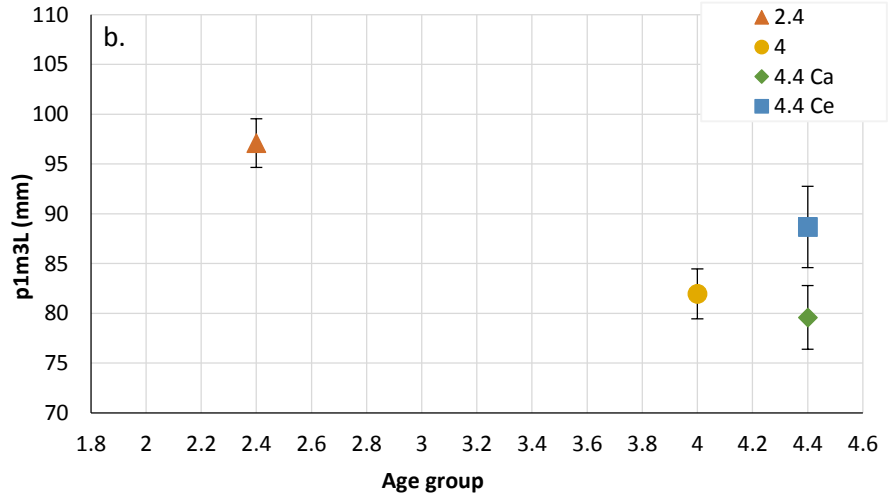


Figure 5.26. p1m3L from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

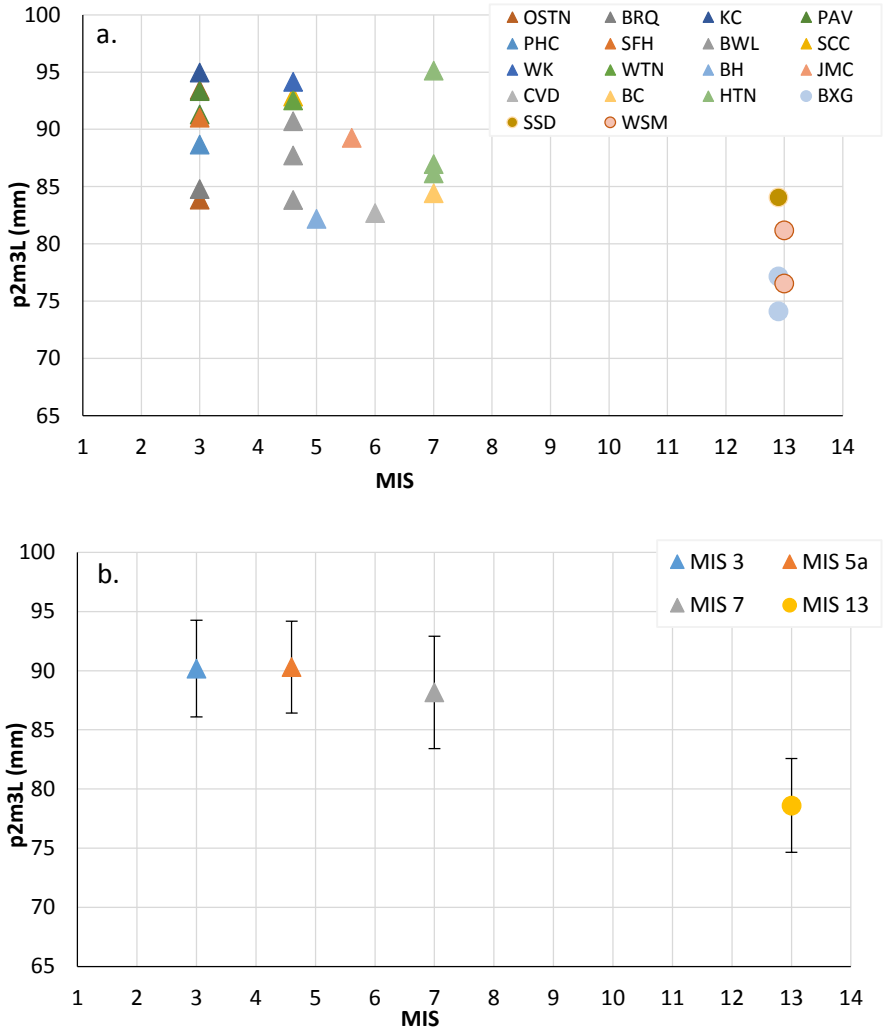


Figure 5.27. p2m3L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

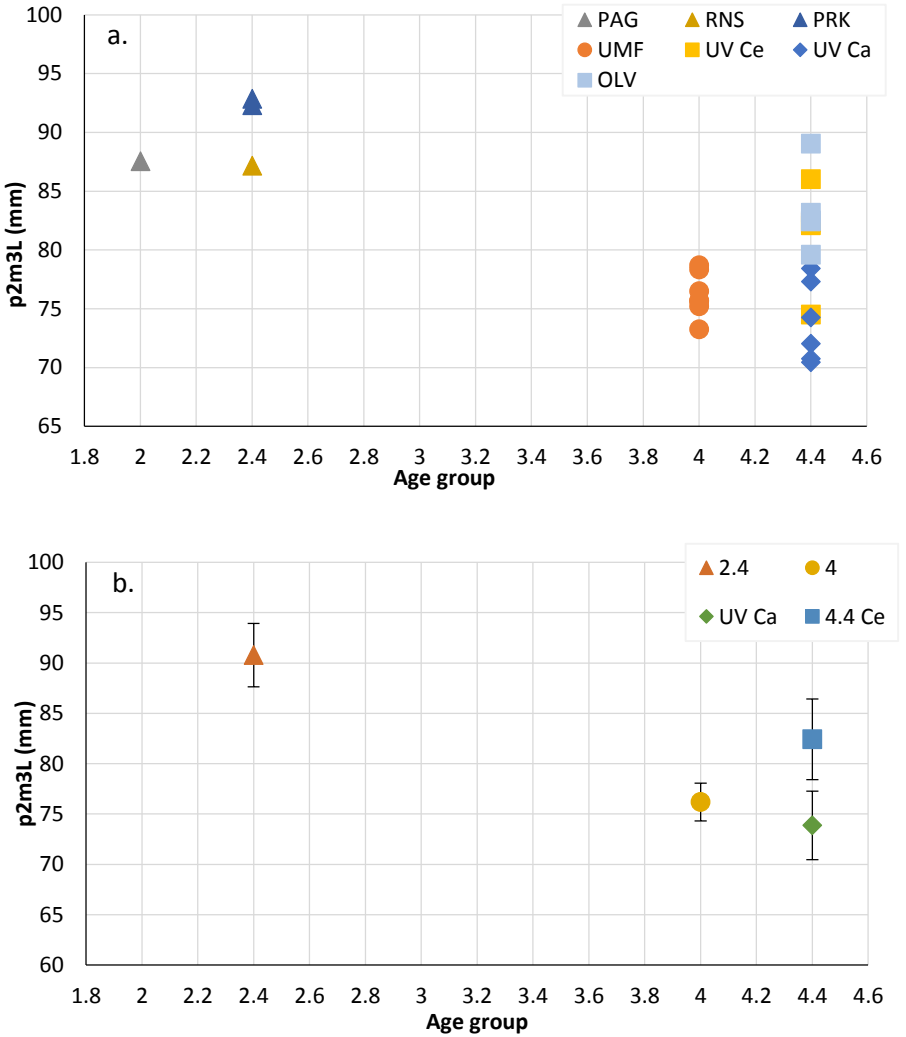


Figure 5.28. p2m3L from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

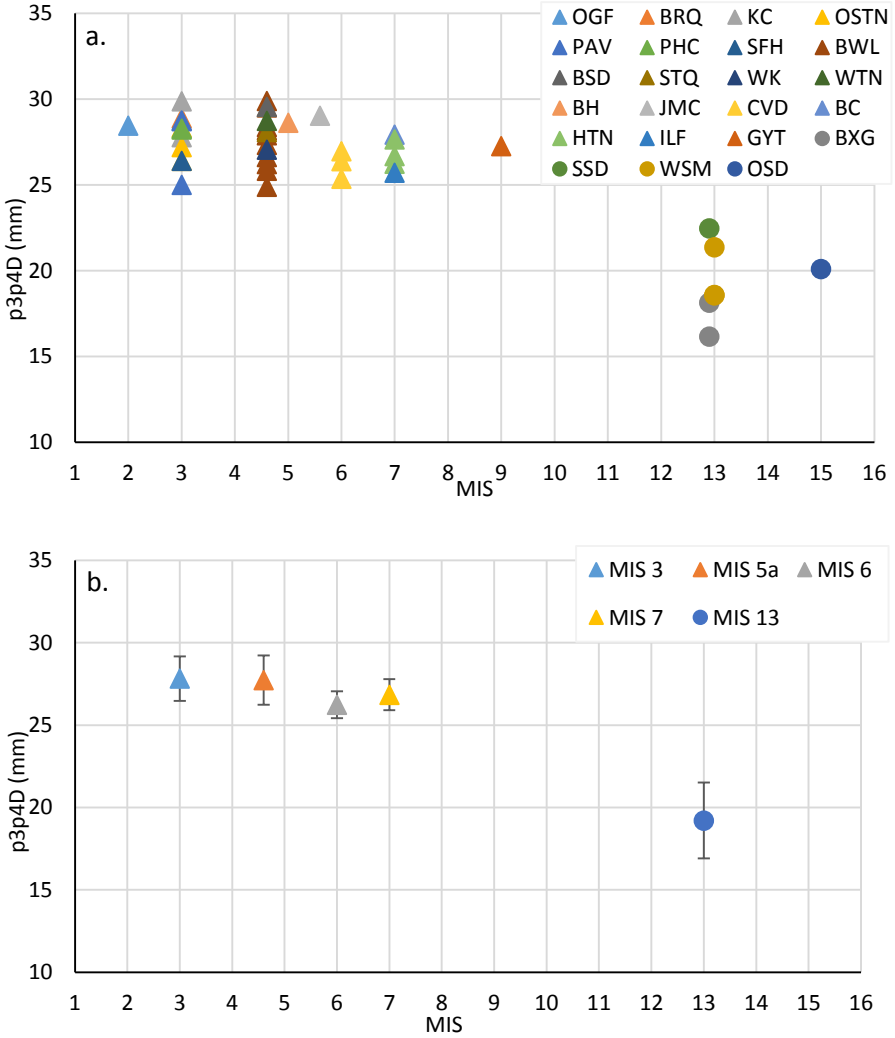


Figure 5.29. p3p4D from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

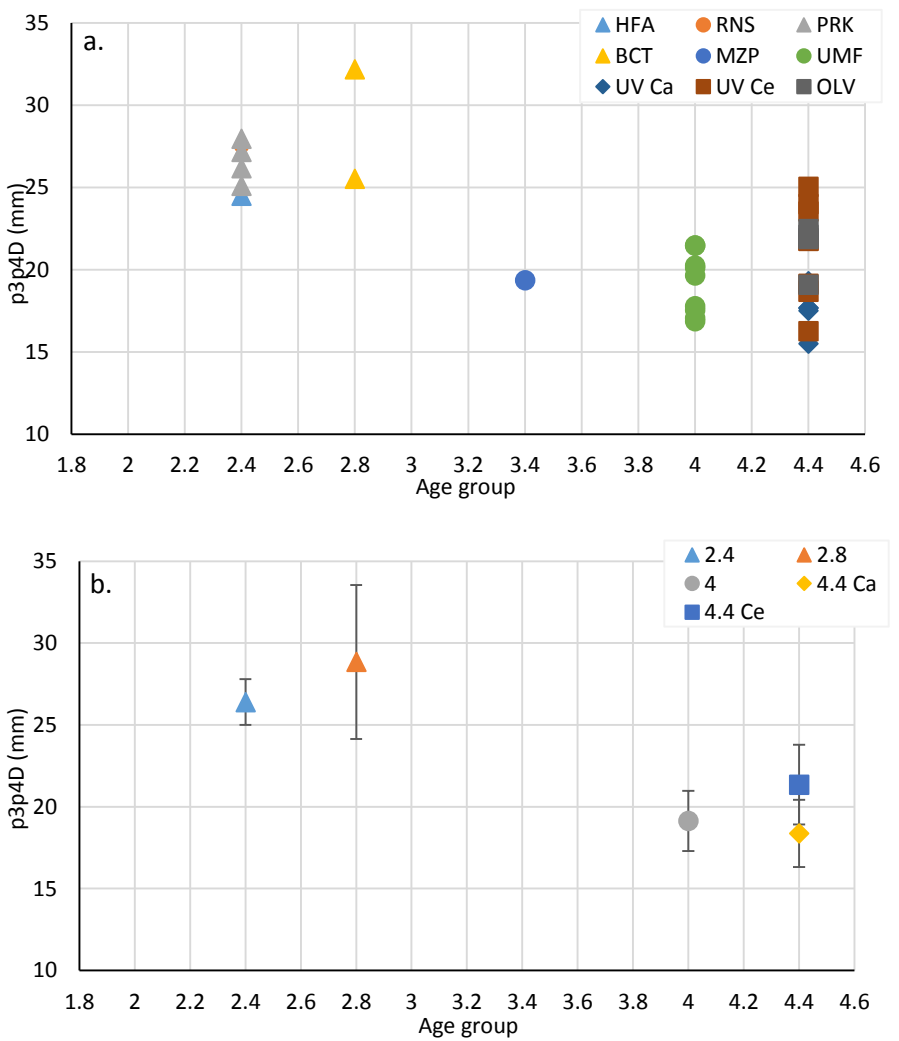


Figure 5.30. p3p4D from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

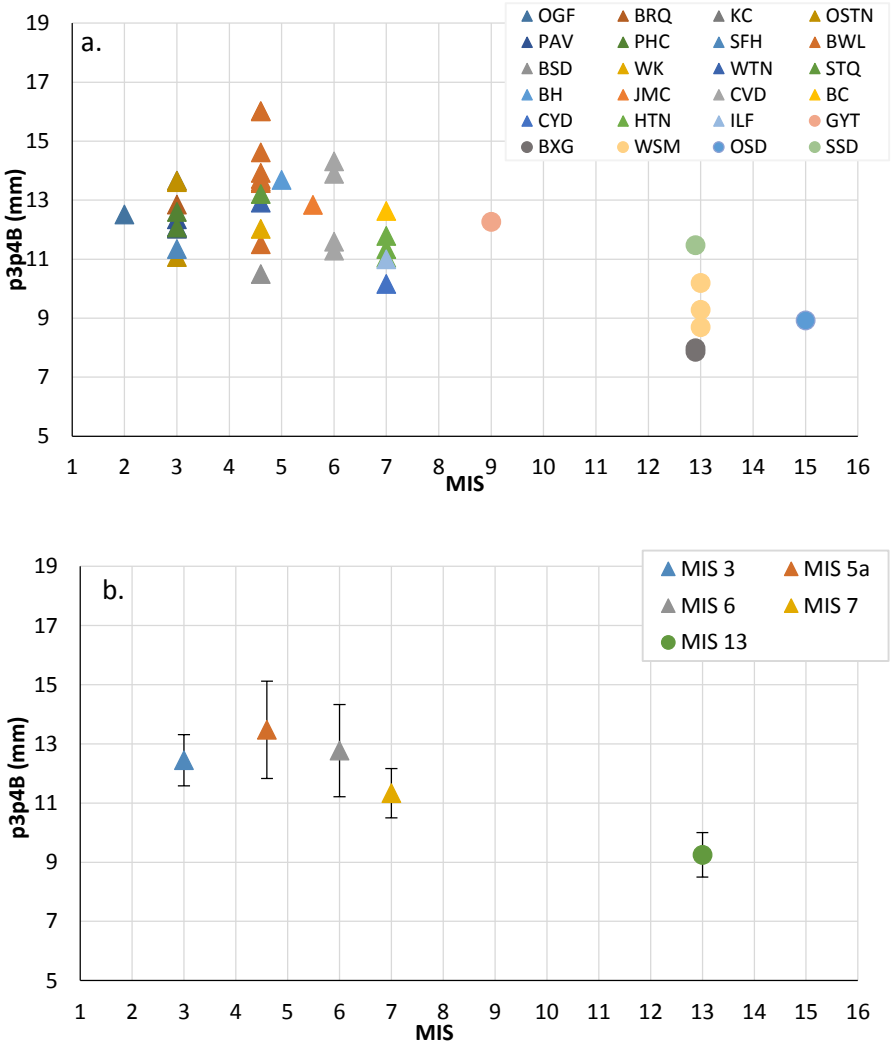


Figure 5.31. p3p4B from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

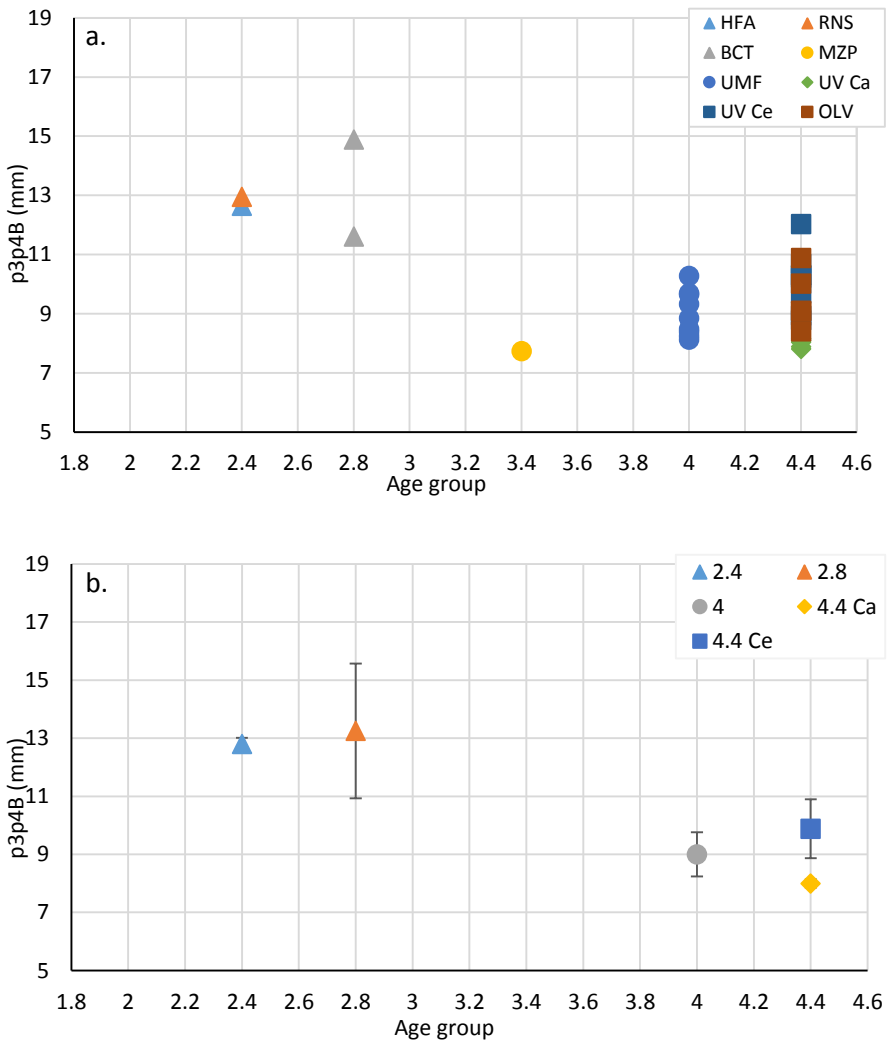


Figure 5.32. p3p4B from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

5.1.5.7. Jaw depth and breadth at the m1-m2 junction (m1m2B and m1m2D)

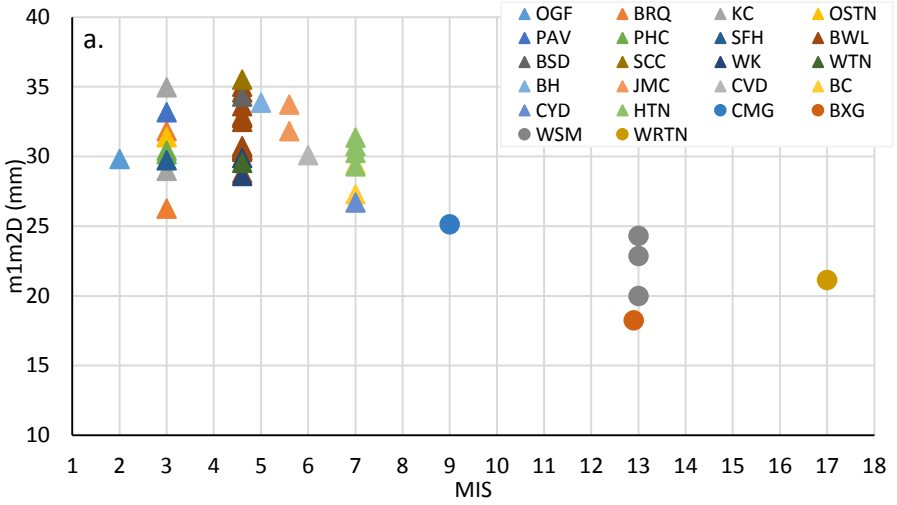
Figures 5.33 and 5.34 compare m1m2D, and Figures 5.35 and 5.36 compare m1m2B in sites and between age groups in Britain and mainland Europe. Large variation is present in *C. lupus* from Britain (the most data-rich area). *C. lupus* generally has broader and deeper jaws (at m1-m2) than all other species, which again overlap as they did with p3p4D and p3p4B. *C. lupus* from MIS 7 in Britain has the narrowest and shallowest jaws compared to the younger age groups, overlapping with the largest values from MIS 13 *C. mosbachensis*. When *C. lupus* and *C. mosbachensis* are compared between the Britain and Europe, both species compare well with their regional counterparts.

5.1.5.8. Upper third premolar (P3)

Figures 5.37 and 5.38 compare P3L across sites and age groups in Britain and mainland Europe. Large variation is present in British *C. lupus*, from where there is the most data. Generally, *C. lupus* has longer P3L than the other species, which all overlap. Noticeably short lengths are present in *C. lupus* during MIS 2, 3 and 6 in Britain, all within range of MIS 13 *C. mosbachensis*. Overall, *C. lupus* and *C. mosbachensis* respectively compare well with their regional counterparts.

5.1.5.9. Upper carnassial (P4)

Figures 5.39 and 5.40 compare P4L, and Figures 5.41 and 5.42 compare P4W between sites and age groups in Britain and mainland Europe. Variation is highest in *C. lupus*, especially in P4W. Generally, *C. lupus* has longer and wider P4 than the other species. *C. mosbachensis* and *C. etruscus* are similar in P4, whilst *C. arnensis* has the smallest P4 overall. *C. lupus* from MIS 5a in Britain has the largest P4, although within the variation of the other age groups. Overall, *C. lupus* and *C. mosbachensis* respectively are similar to their regional counterparts.



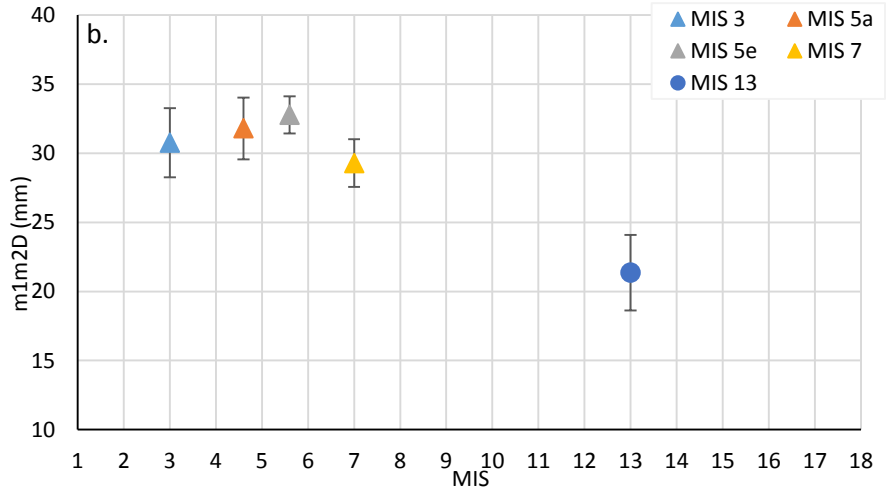
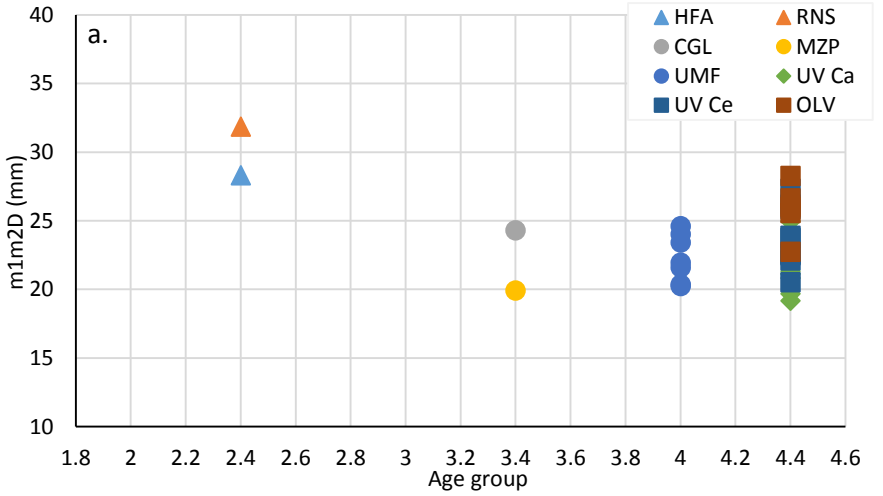


Figure 5.33. m1m2D from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.



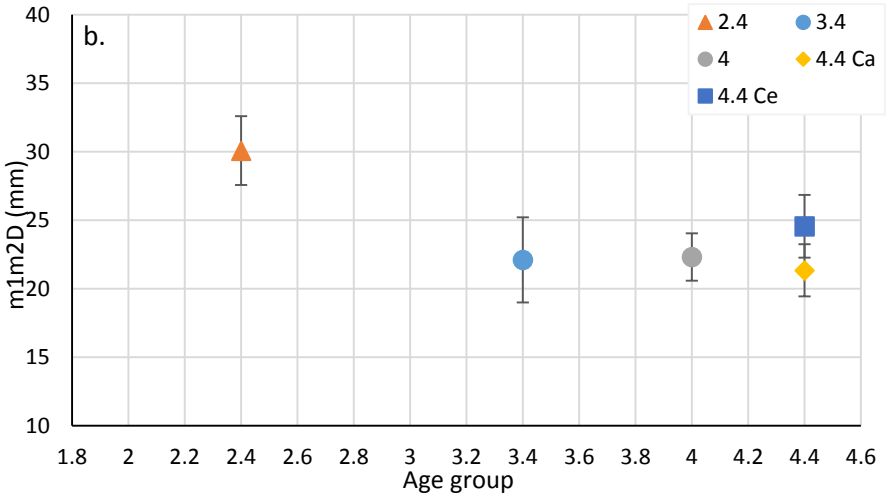


Figure 5.34. m1m2D from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

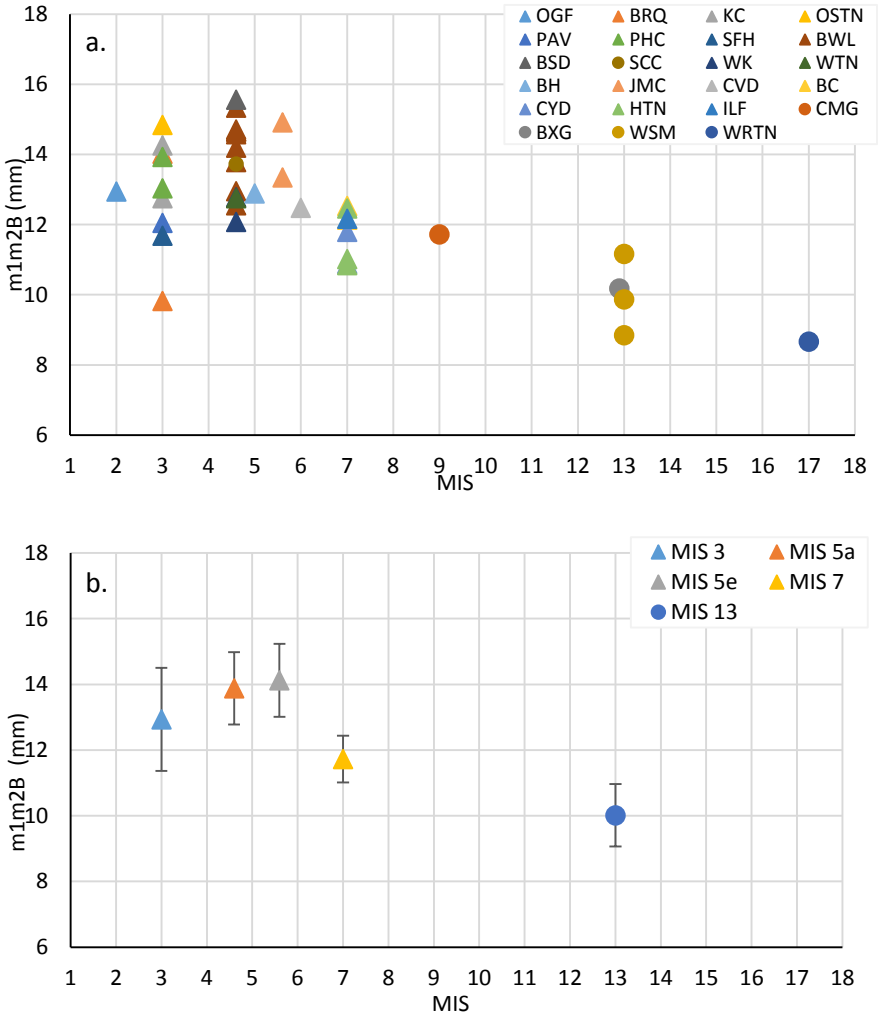


Figure 5.35. m1m2B from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

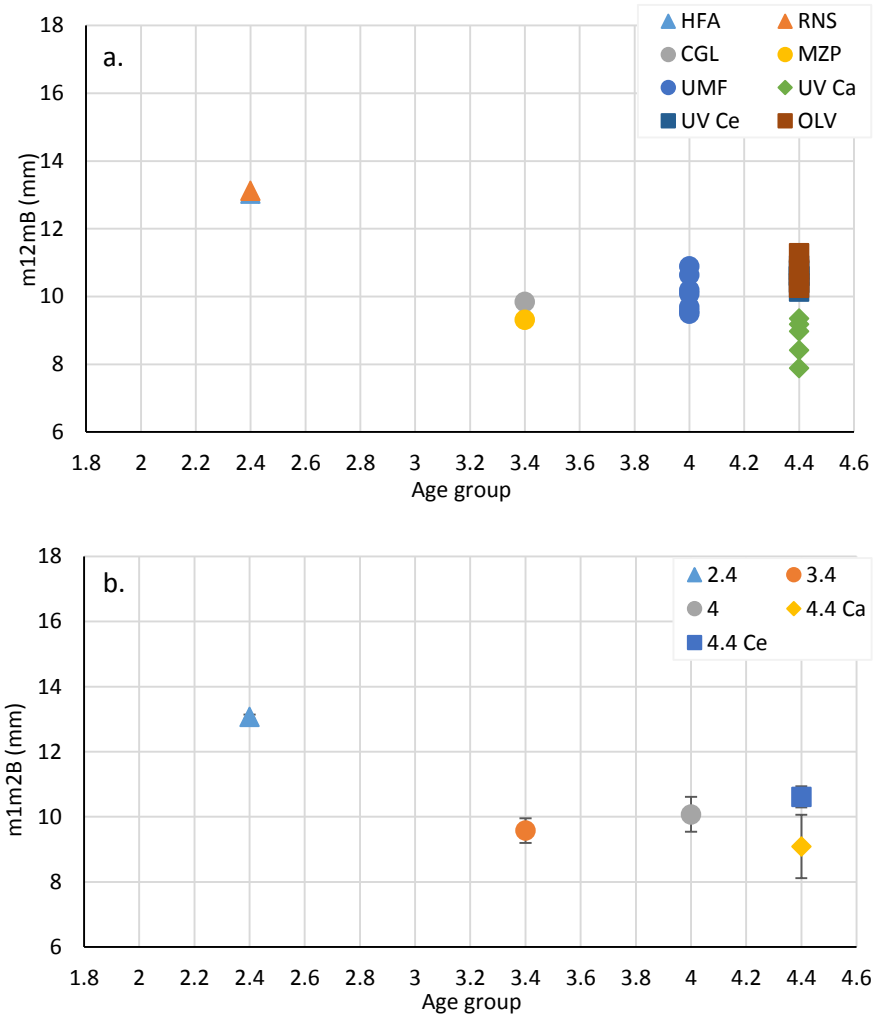
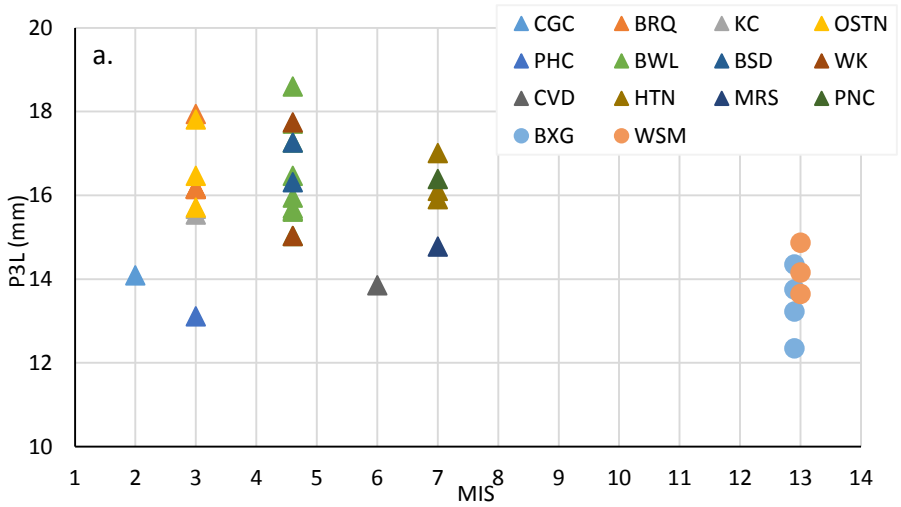


Figure 5.36. m1m2B from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊



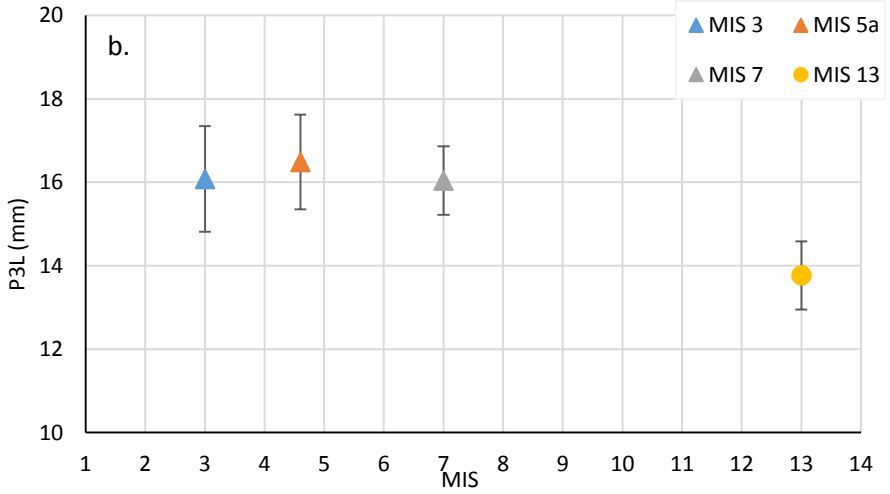
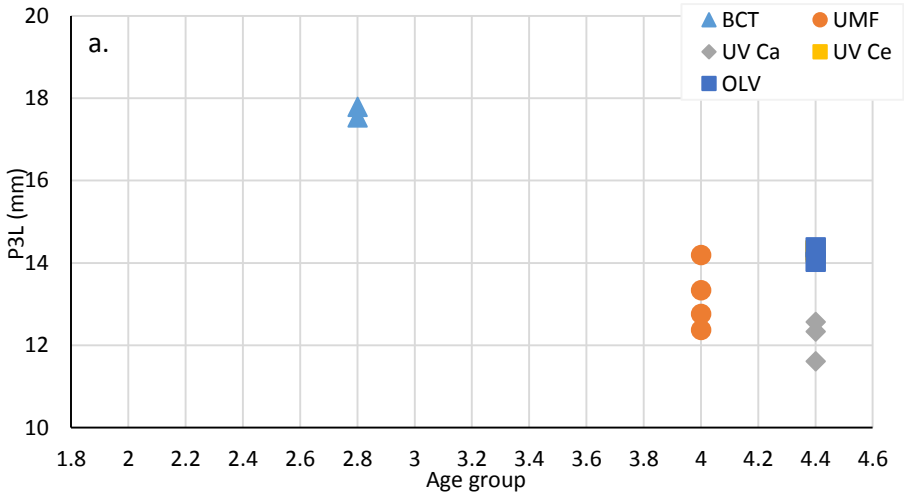


Figure 5.37. P3L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.



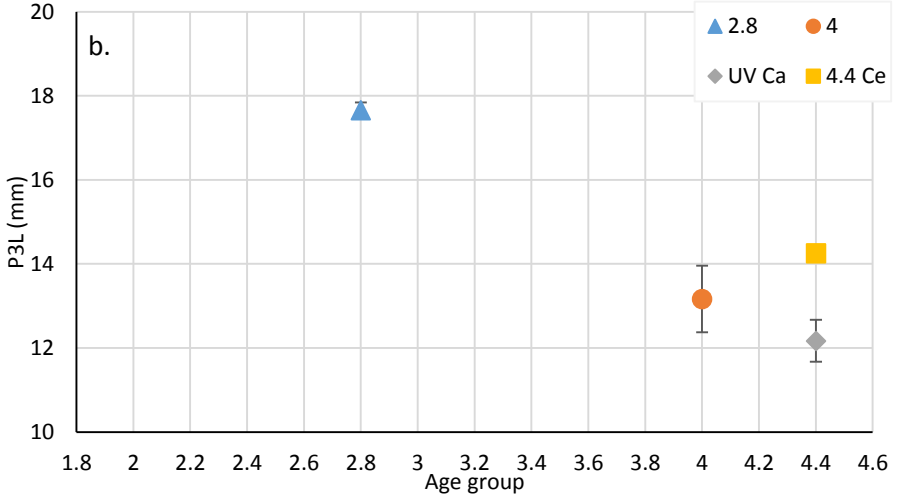
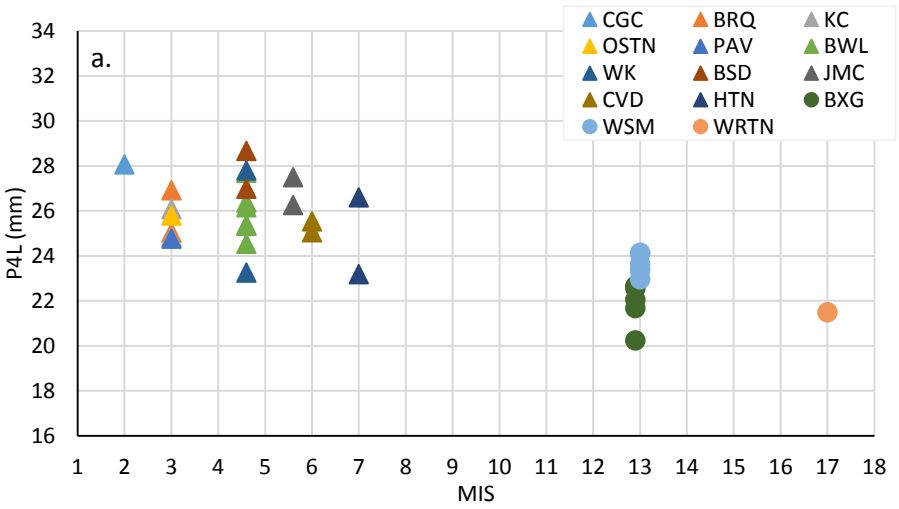


Figure 5.38. P3L from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊



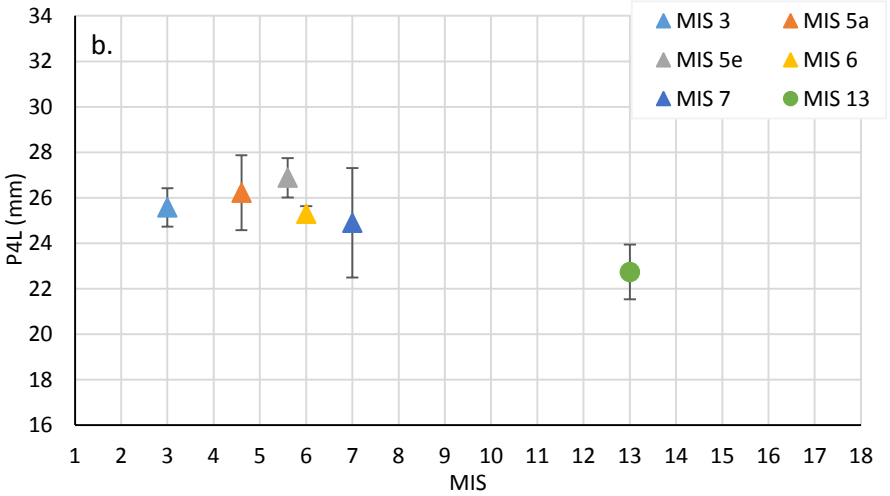
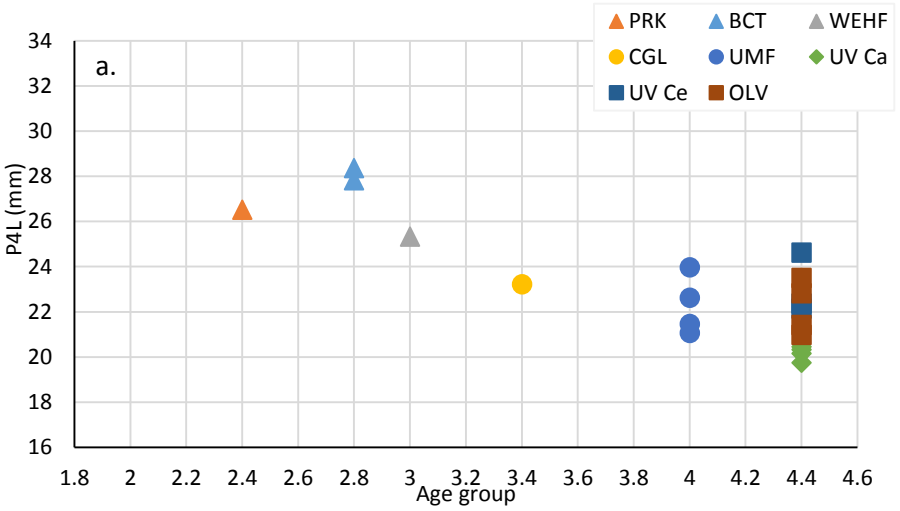


Figure 5.39. P4L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.



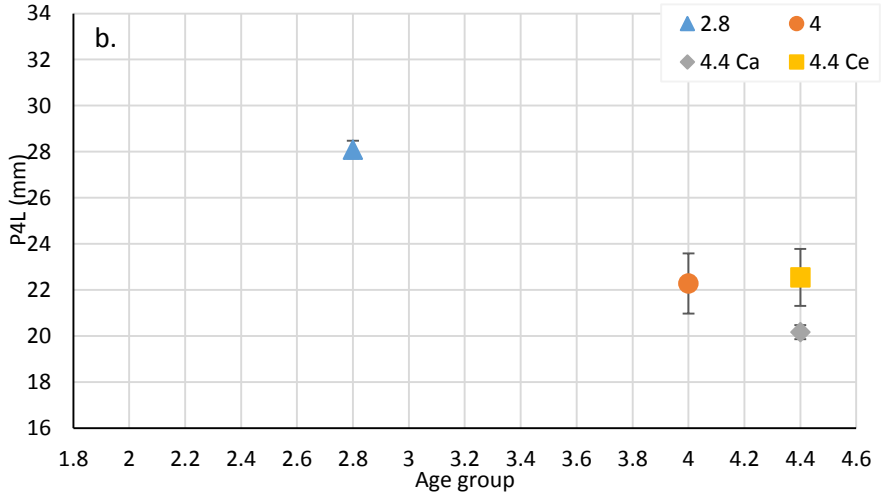


Figure 5.40. P4L from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

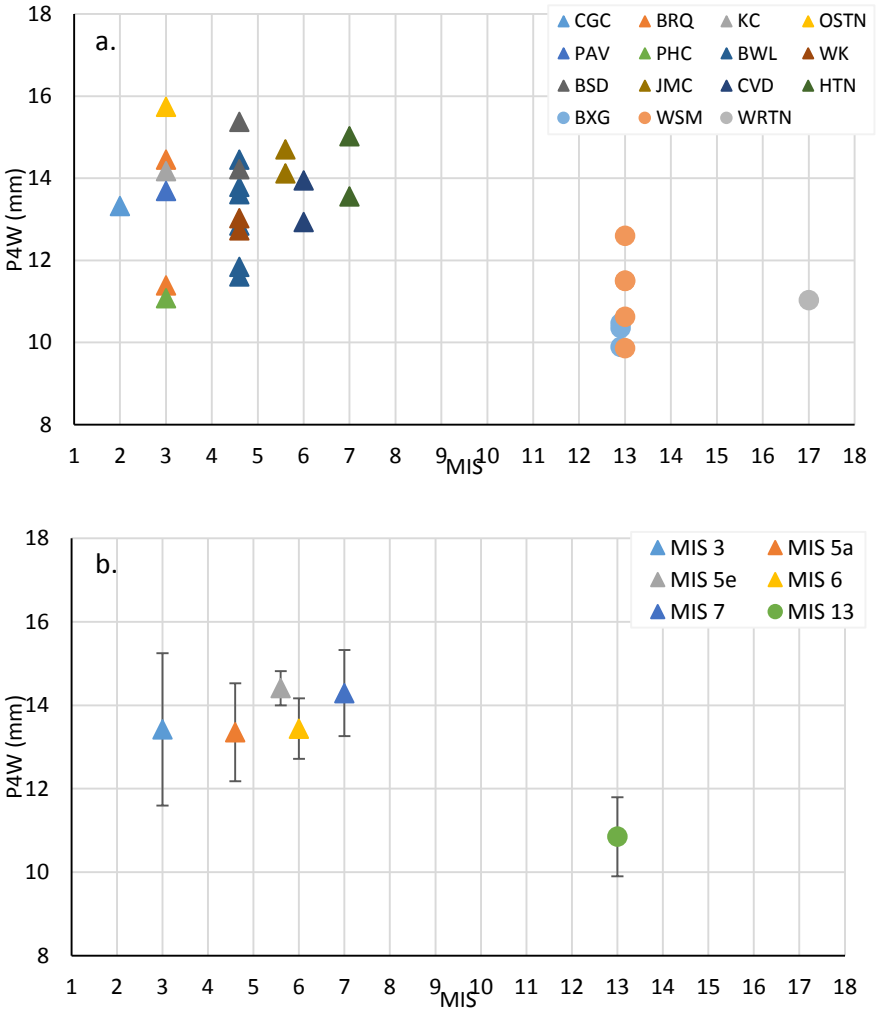


Figure 5.41. P4W from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

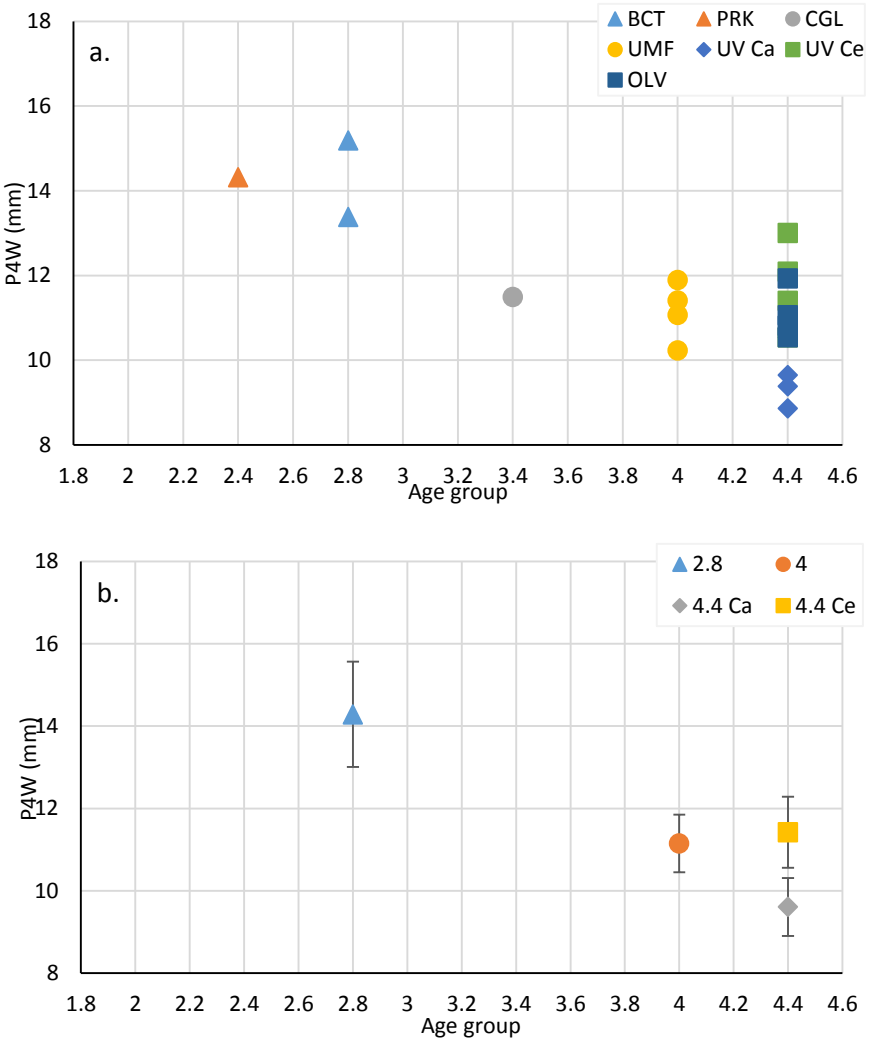


Figure 5.42. P4W from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

5.1.5.10. Upper first molar (M1)

Figures 5.43 and 5.44 compare M1L, and Figures 5.45 and 5.46 compare M1W in sites and between age groups in Britain and mainland Europe. Large variation is present in the rich dataset of British *C. lupus*. Generally, *C. lupus* has longer and wider M1 than *C. mosbachensis* and *C. arnensis*. *C. lupus* and *C. etruscus* overlap, as do *C. mosbachensis* and *C. arnensis*. *C. lupus* from MIS 3 and 5a in Britain were the most varied, whilst the remaining age groups were more similar. *C. lupus* from the early Late Pleistocene in Europe (age group 2.8) contained the largest M1 overall. Generally, *C. lupus* and *C. mosbachensis* respectively are similar to their regional counterparts.

5.1.5.11. Upper second molar (M2)

Figures 5.47 and 5.48 compare M2W between sites and age groups in Britain and mainland Europe. *C. mosbachensis* shows large variation in M2W, with *C. lupus* comparatively less. Generally *C. lupus* has wider M2 than the other species, although *C. mosbachensis* overlaps in its variation. *C. mosbachensis, C. arnensis* and *C. etruscus* are all more similar in M2W. *C. lupus* from the early Late Pleistocene (age group 2.8) in Europe has wider M2W compared to Britain. General regional similarity is shown between *C. lupus* and *C. mosbachensis* respectively.

5.1.5.12. Upper premolar row (P1P4L)

Figures 5.49 and 5.50 compare P1P4L in sites and between age groups in Britain and mainland Europe. Large variation in present in *C. lupus* from Britain, from where there is most data. *C. lupus* has slightly longer P1P4L than all other species, although there is considerable overlap. *C. mosbachensis* overlaps with both *C. arnensis* and *C. etruscus*, whilst *C. etruscus* is clearly separate from *C. arnensis*. MIS 3 *C. lupus* contains the highest variation in P1P4L, and has similar mean value as MIS 7 *C. lupus*. MIS 5a *C. lupus* has the longest P1P4L. Although the European sites are data-deficient in this measurement, *C. mosbachensis* from Britain and Europe appear similar.

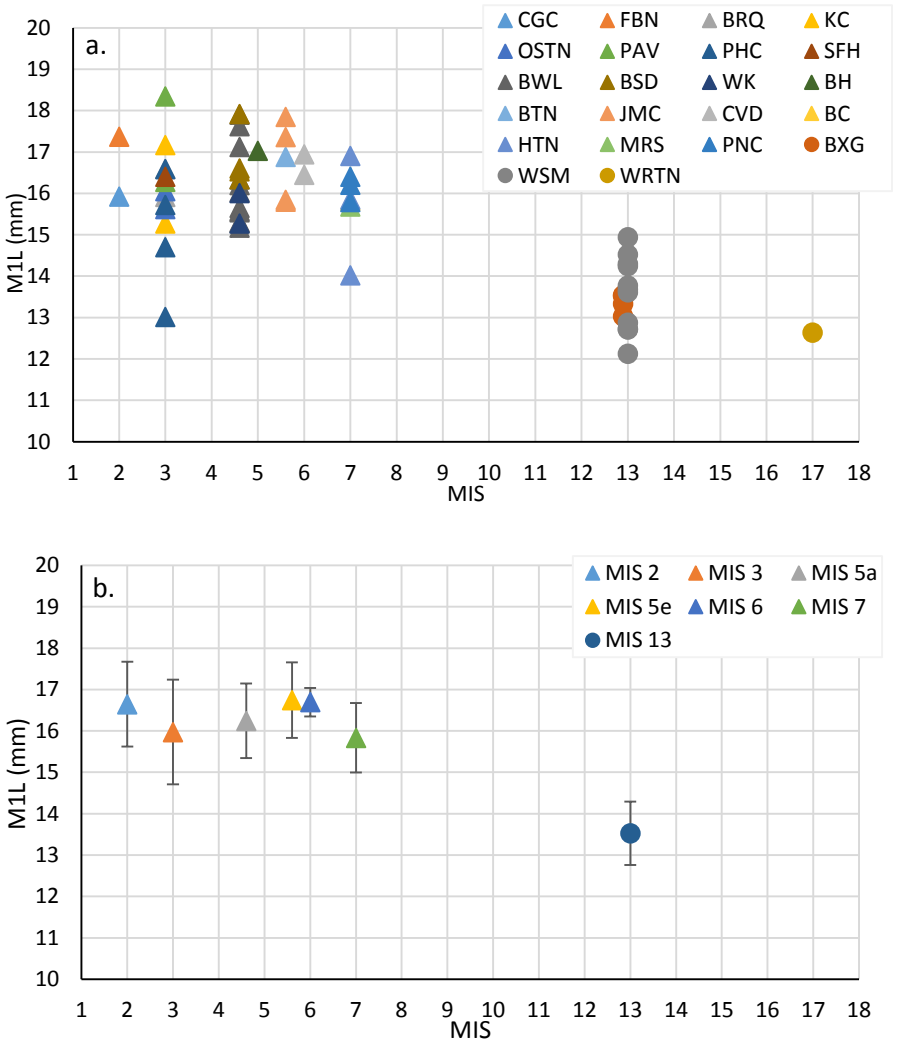


Figure 5.43. M1L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

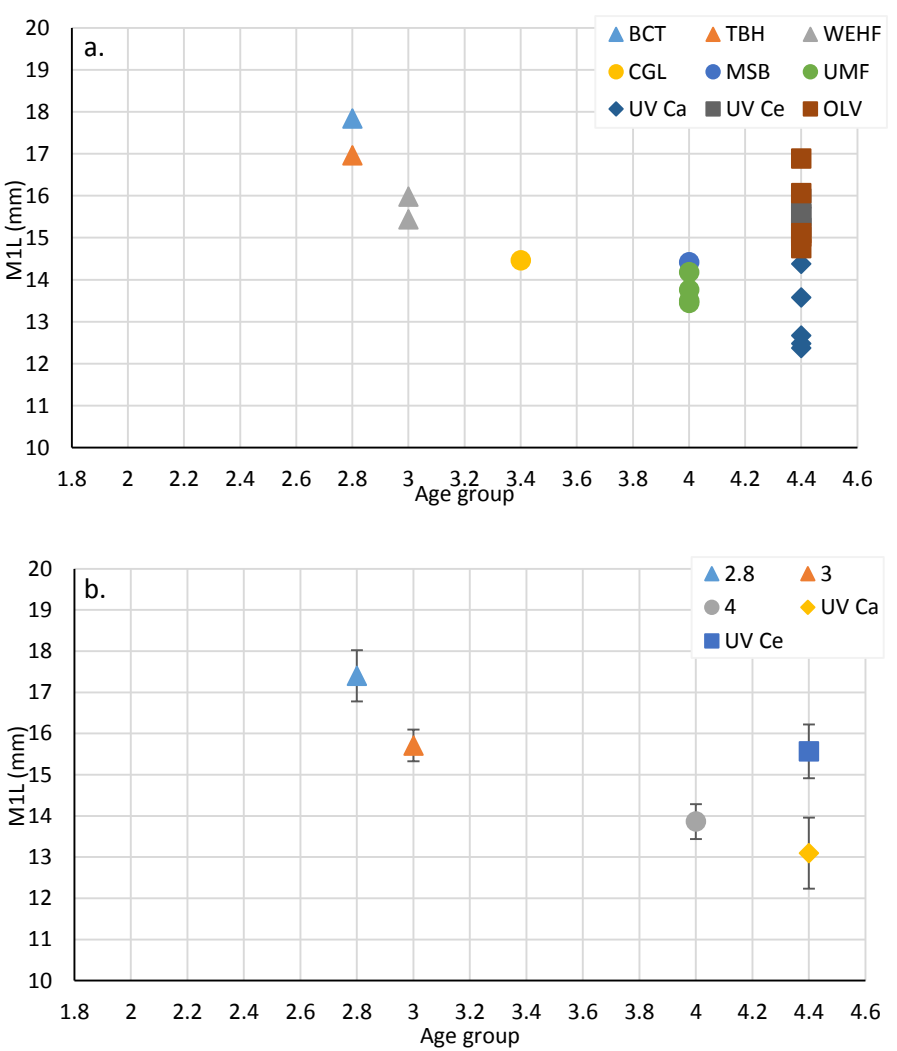


Figure 5.44. M1L from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

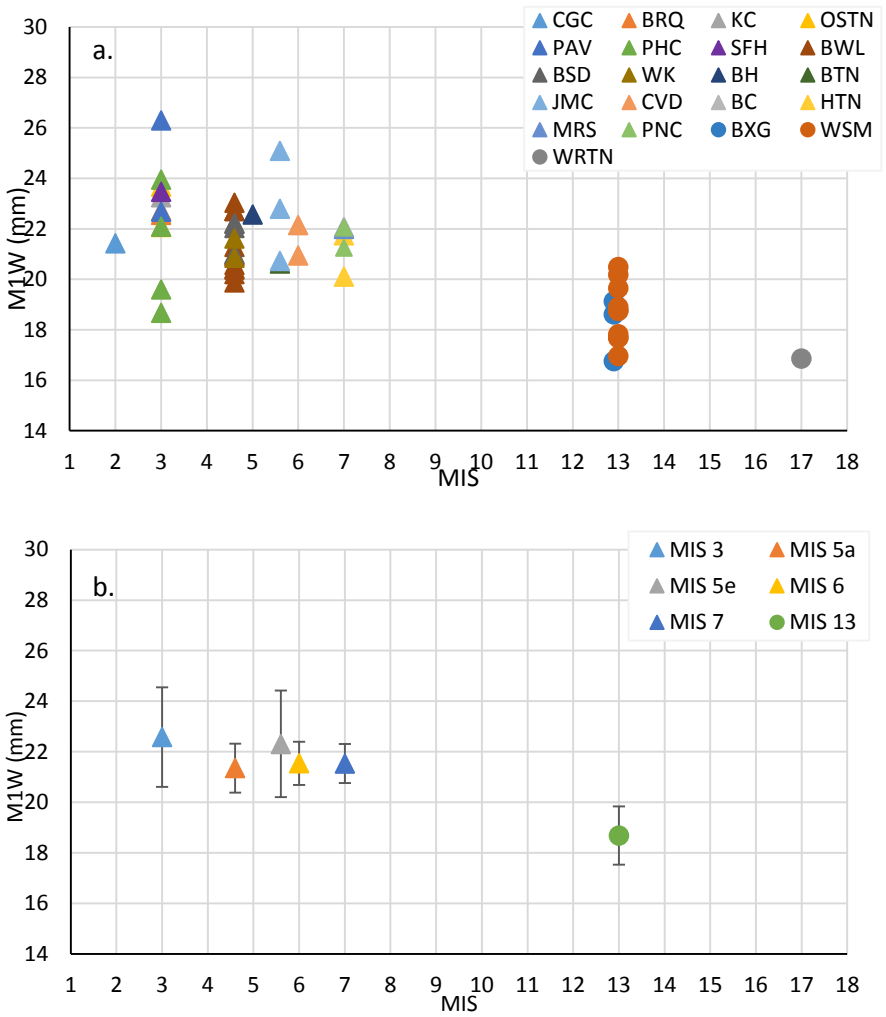


Figure 5.45. M1W from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

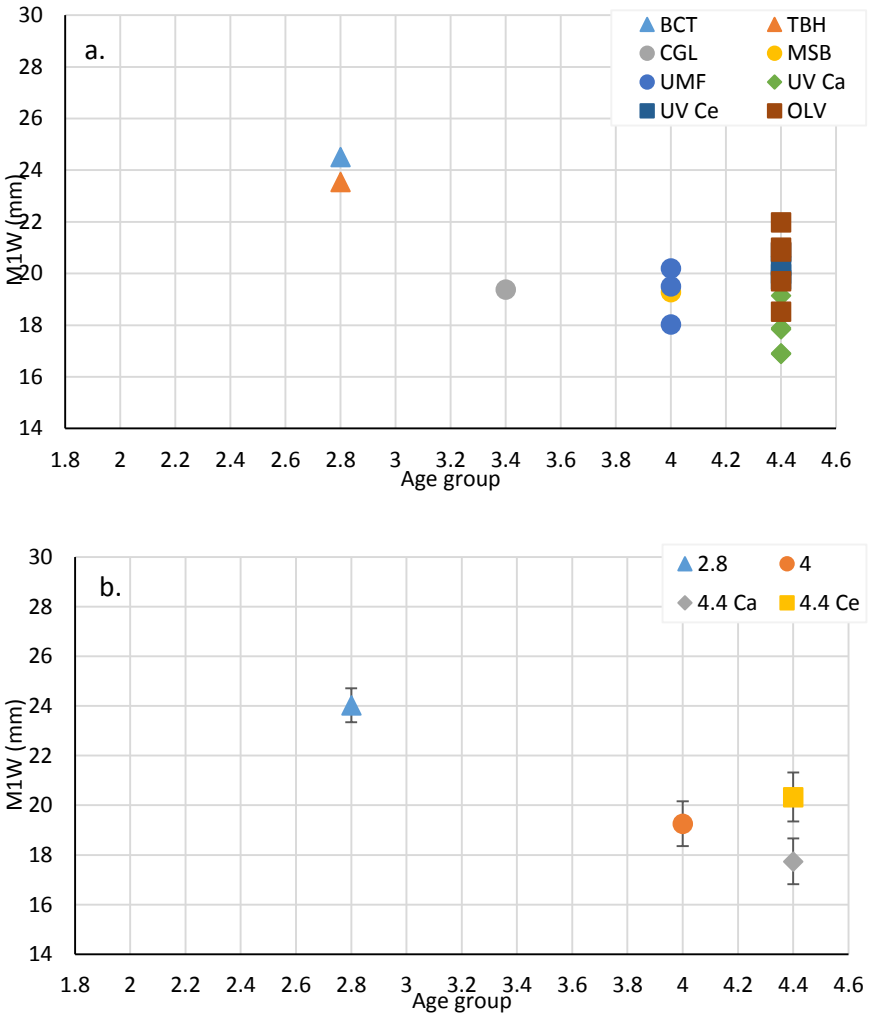


Figure 5.46. M1W from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

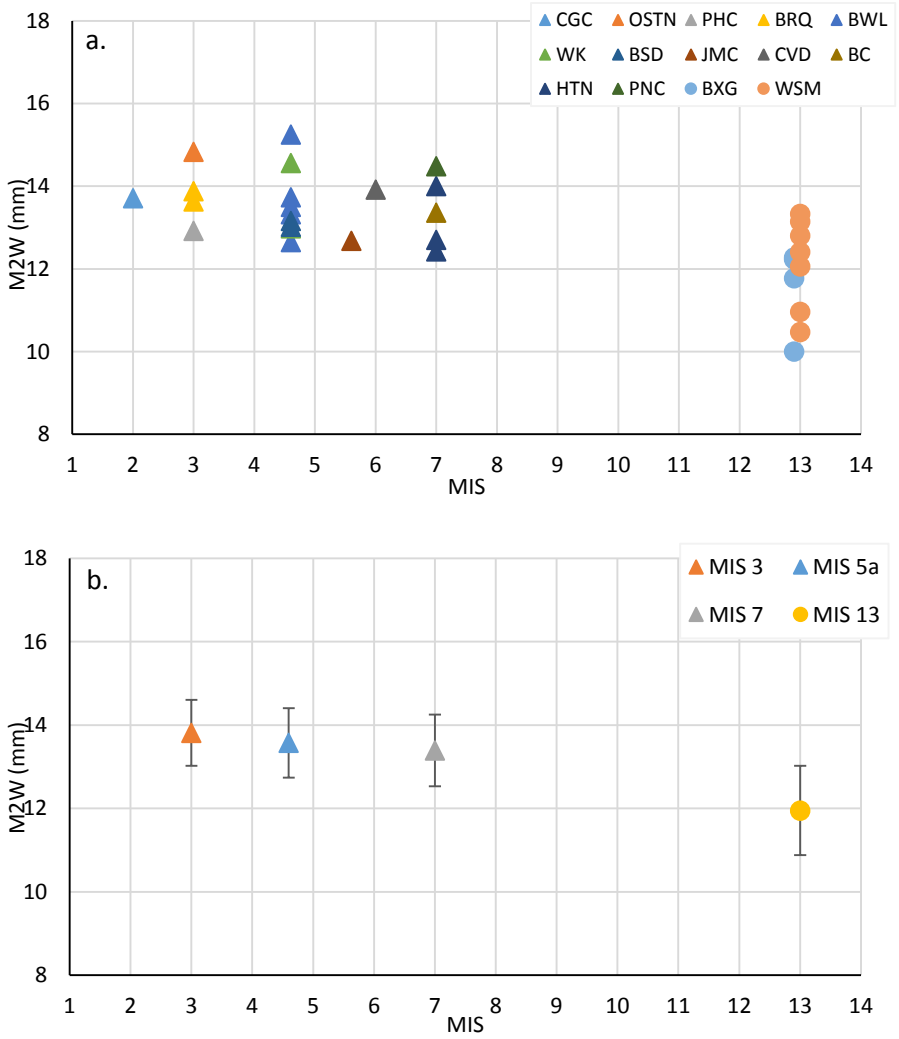


Figure 5.47. M2W from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

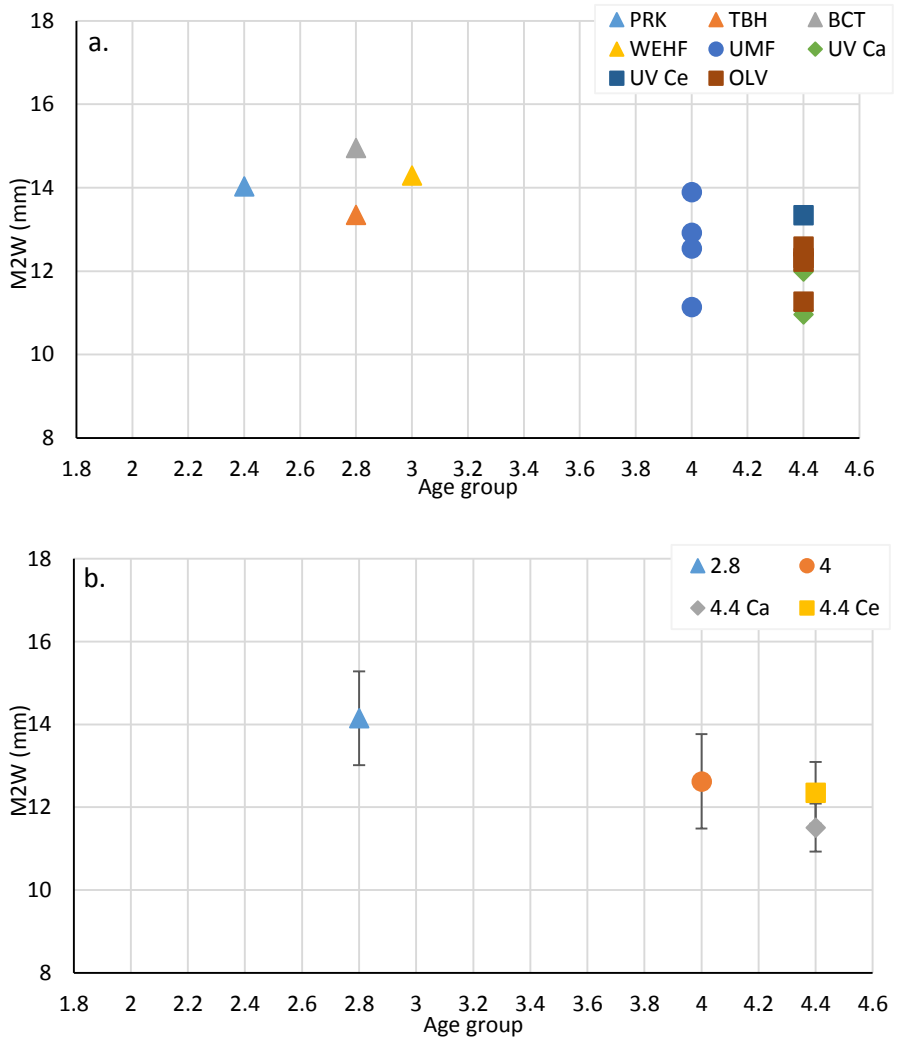
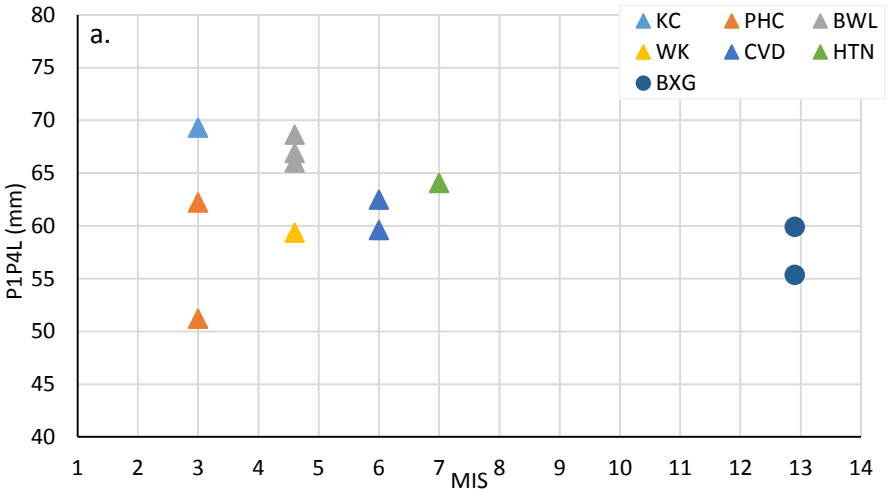


Figure 5.48. M2W from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊



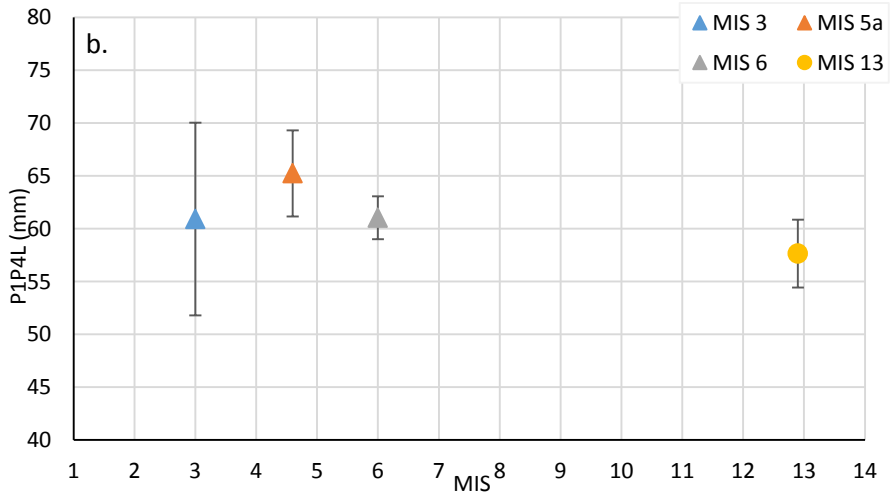
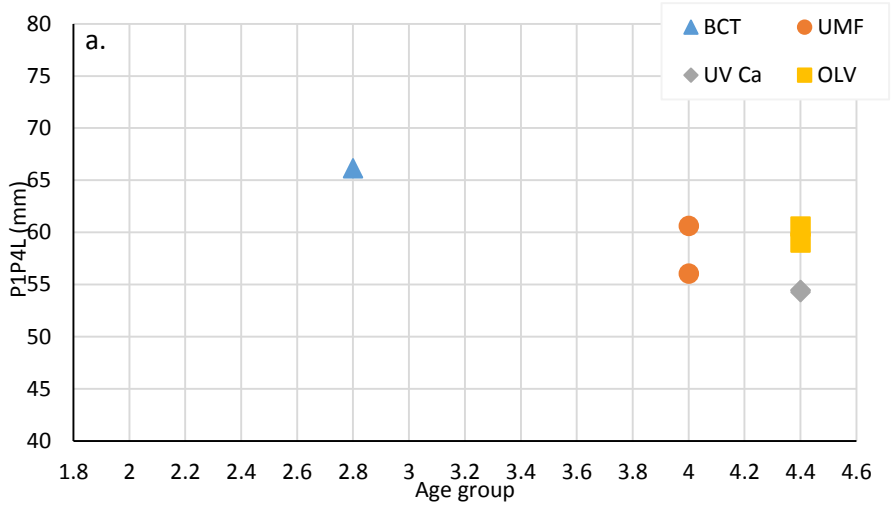


Figure 5.49. P1P4L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.



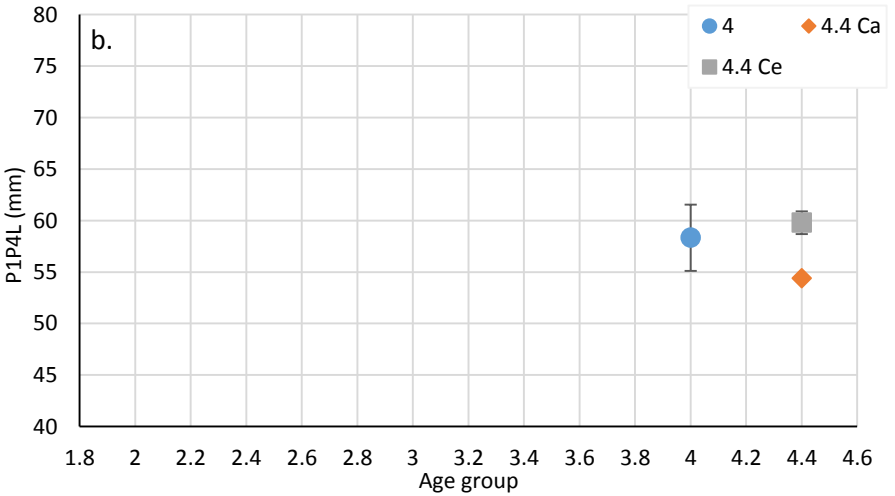


Figure 5.50. P1P4L from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

5.1.5.13. Upper cheek tooth row (P1M2L)

Figure 5.51 and 5.52 compare P1M2L between sites and age groups in Britain and mainland Europe. Large variation in present in *C. lupus* from Britain, where there is the most data. *C. lupus* has longer mean P1M2L than all other species, although overlap is present in variation with European *C. mosbachensis*. Not enough data are present to compare *C. etruscus. C. mosbachensis* has longer P1M2L than *C. arnensis*. Within Britain, MIS 3 *C. lupus* has longer mean P1M2L than those from MIS 5a, although they overlap in variation. Comparisons between *C. lupus* and *C. mosbachensis* respectively from Britain and Europe were not possible.

5.1.5.14. Upper tooth row (C1M2L)

Figures 5.53 and 5.54 compare C1M2L between sites and age groups in Britain and mainland Europe. Large variation is present in *C. lupus* from Britain, where the majority of data is from. Generally, *C. lupus* has longer C1M2L than *C. mosbachensis* and *C. arnensis*. There was not enough data from *C. etruscus* to compare. *C. mosbachensis* had longer C1M2L than *C. arnensis*. An individual from Hutton Cave had the longest C1M2L in comparison to other Pleistocene *C. lupus*. MIS 3 and 5a *C. lupus* overlapped in variation. Comparisons between *C. lupus* and *C. mosbachensis* respectively from Britain and Europe were not possible.

5.1.5.15. Upper molar length (M1M2L)

Figures 5.55 and 5.56 compare M1M2L in sites and between age groups in Britain and mainland Europe. Large variation is present in *C. lupus, C. mosbachensis* and *C. etruscus*. Generally, *C. lupus* has longer M1M2L than *C. arnensis* and *C. mosbachensis* although variation is present. However it is similar to *C. etruscus*. *C. mosbachensis* and *C. etruscus* overlap in their variation, whilst *C. arnensis* is separate with shorter M1M2L. *C. lupus* from the early Late Pleistocene (age group 2.8) in Europe has the longest M1M2L, with remaining *C. lupus* age groups more similar. *C. lupus* compares well between Britain and Europe, as does *C. mosbachensis*.

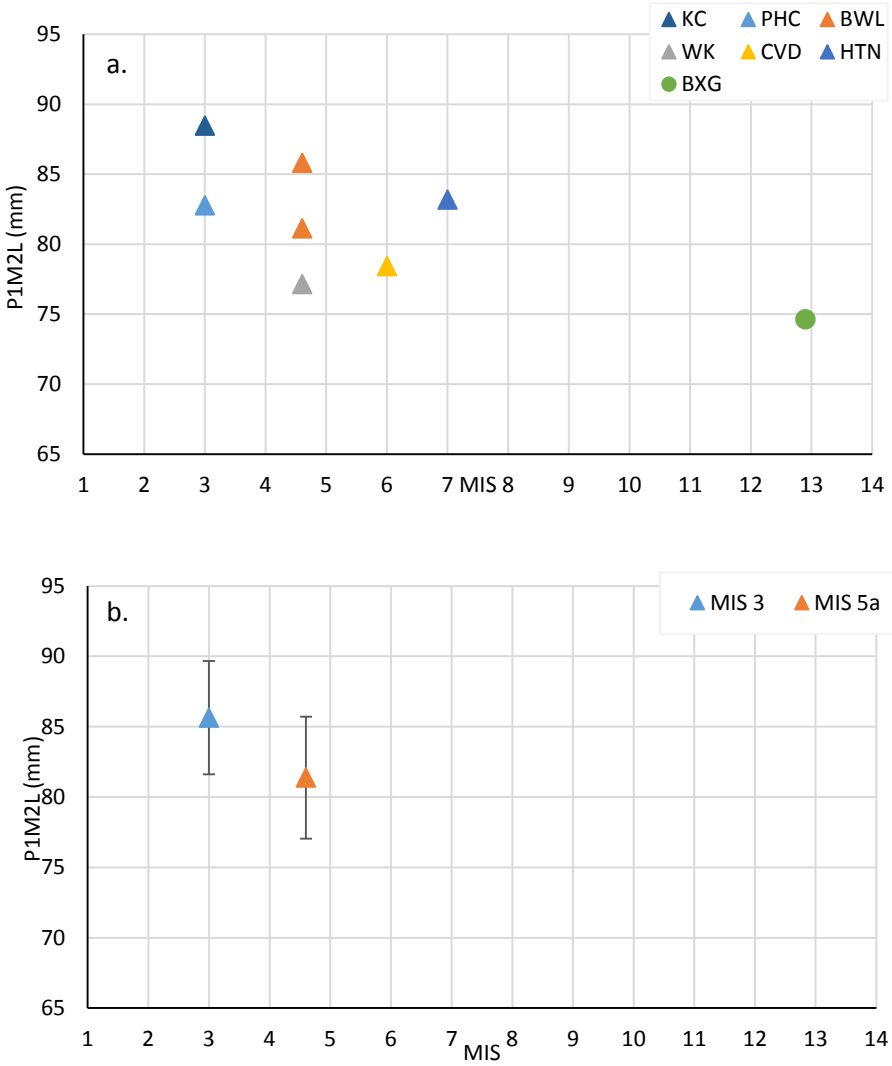


Figure 5.51. P1M2L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

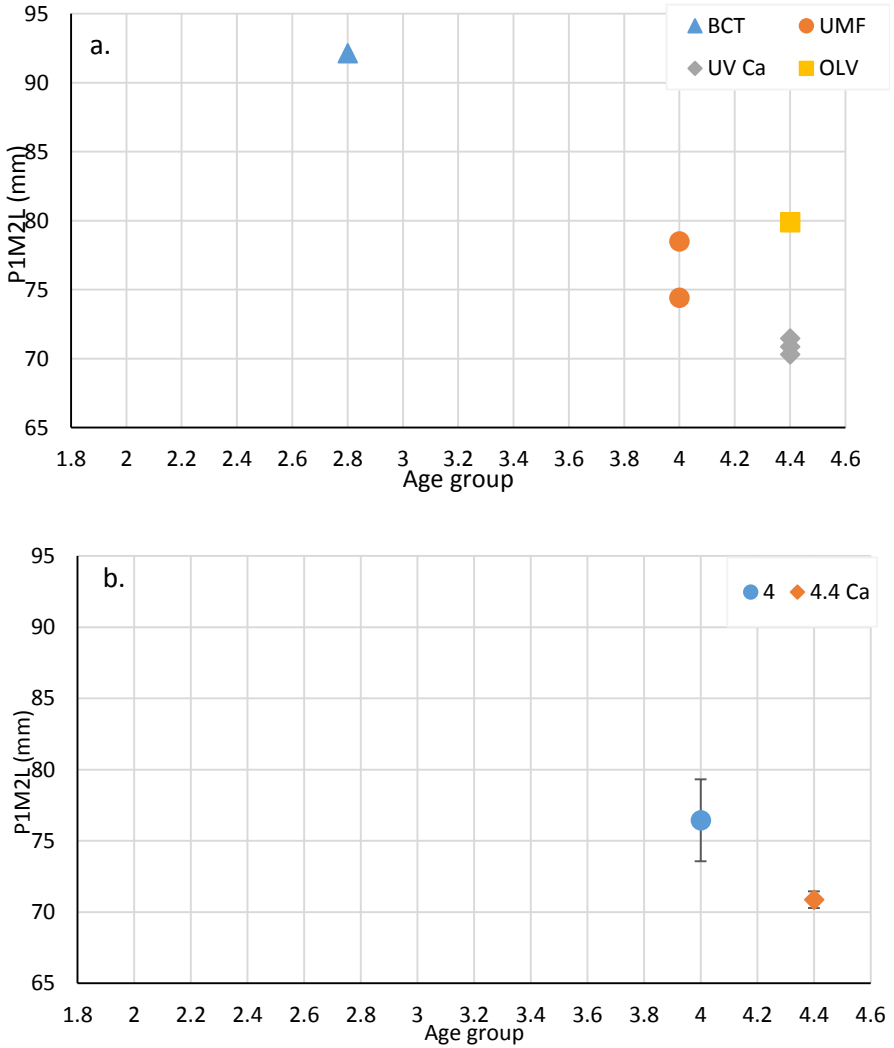


Figure 5.52. P1M2L from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

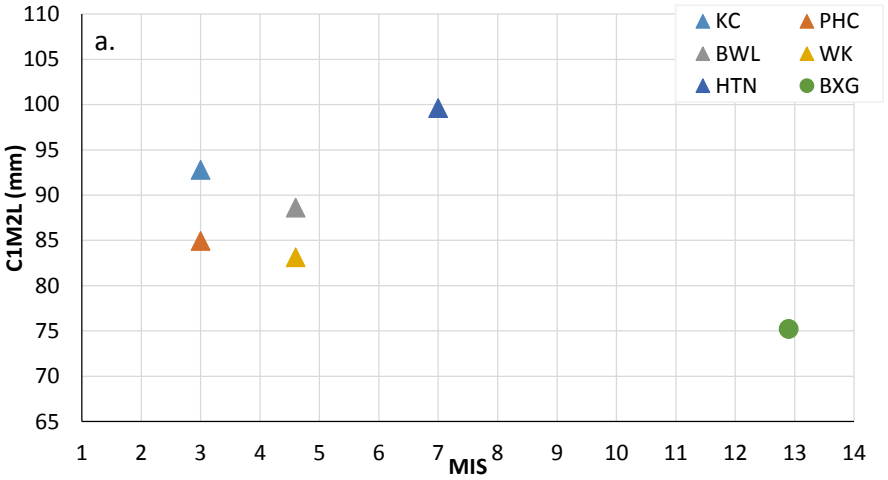


Figure 5.53. C1M2L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.

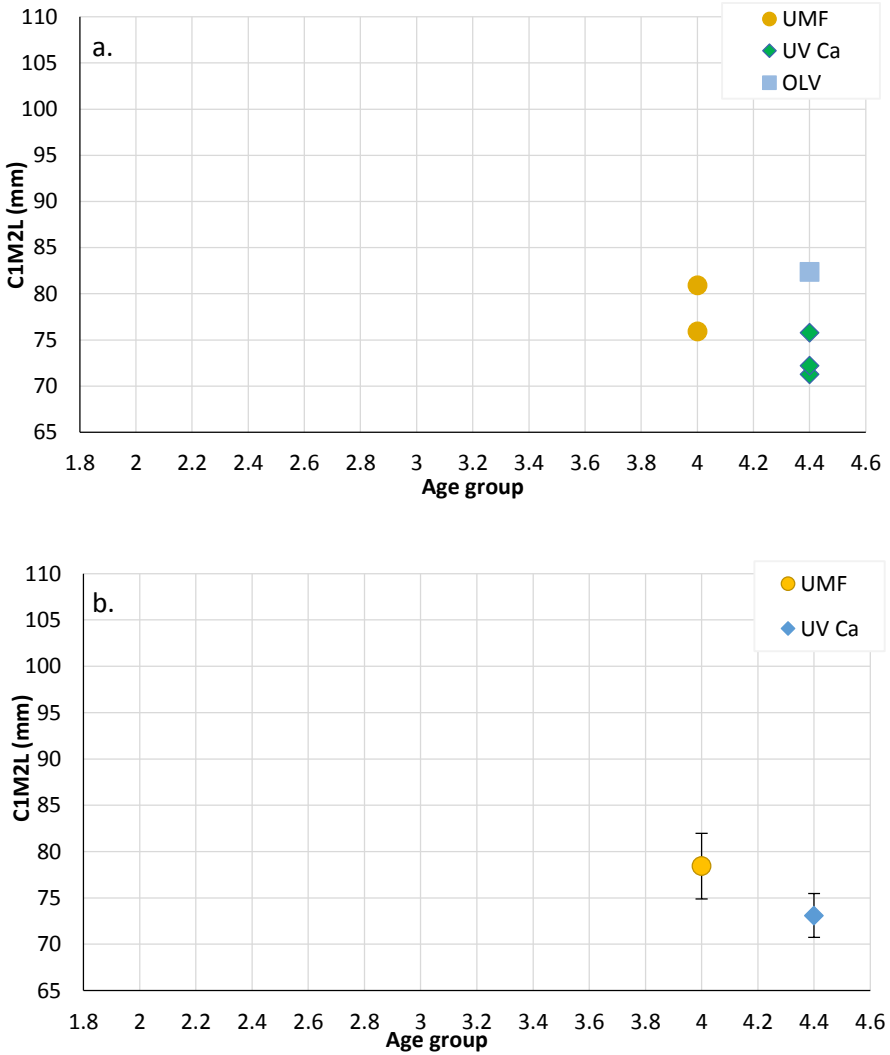
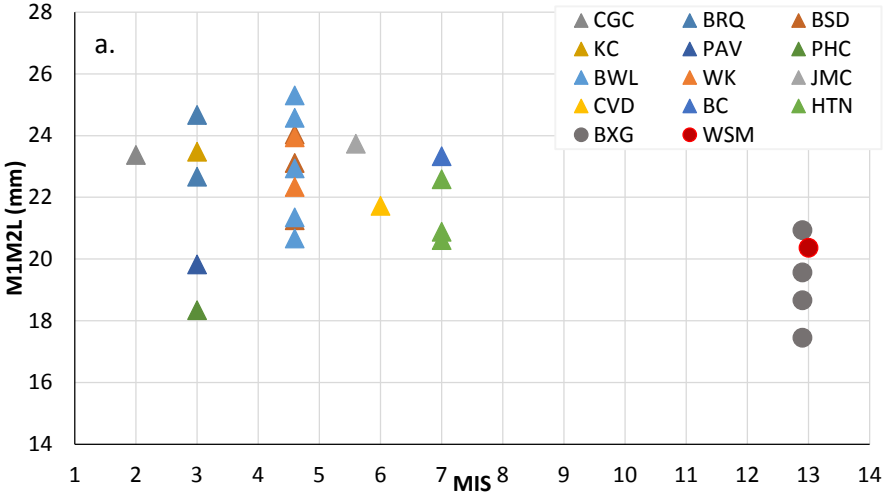


Figure 5.54. C1M2L from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊



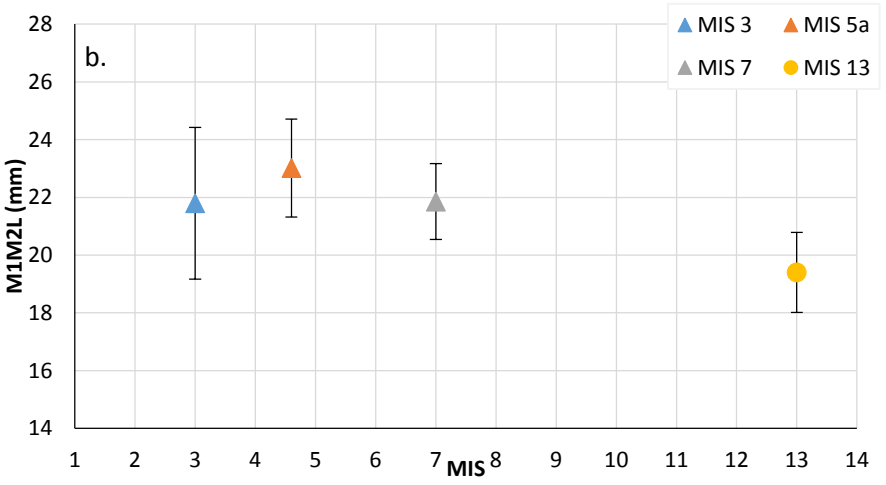
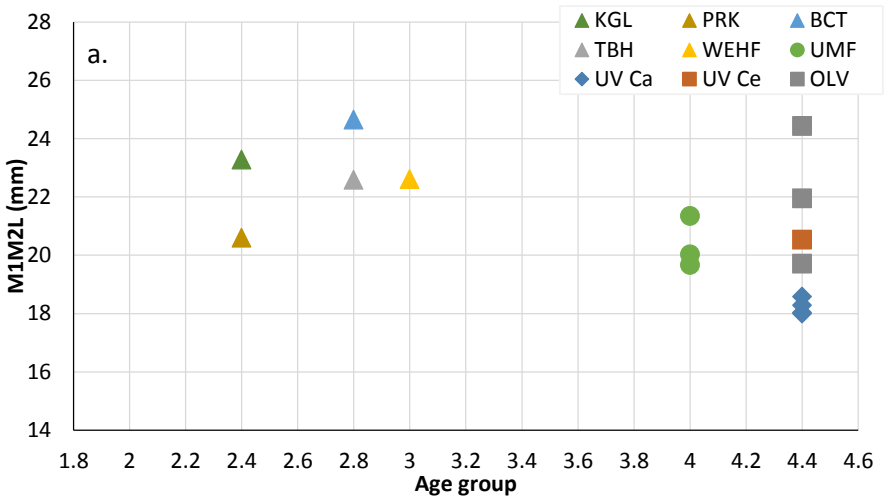


Figure 5.55. M1M2L from Britain a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○.



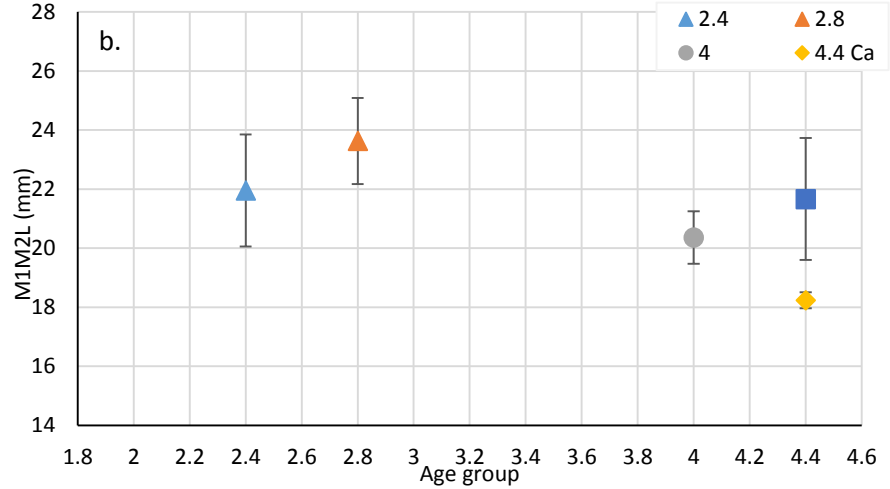


Figure 5.56. M1M2L from European mainland a). individuals from all sites, b). mean and SD for age group. Symbol denotes species; *C. lupus*: Δ, *C. mosbachensis*: ○. *C. etruscus*: □, *C. arnensis*: ◊

5.1.6. Post-cranial material

Complete limb bones can provide inferences on body size. However, whole limbs were generally rare in all sites examined. Figures 5.57, 5.58 and 5.59 illustrate the greatest lengths recorded of *C. lupus* humeri, femora and tibiae.

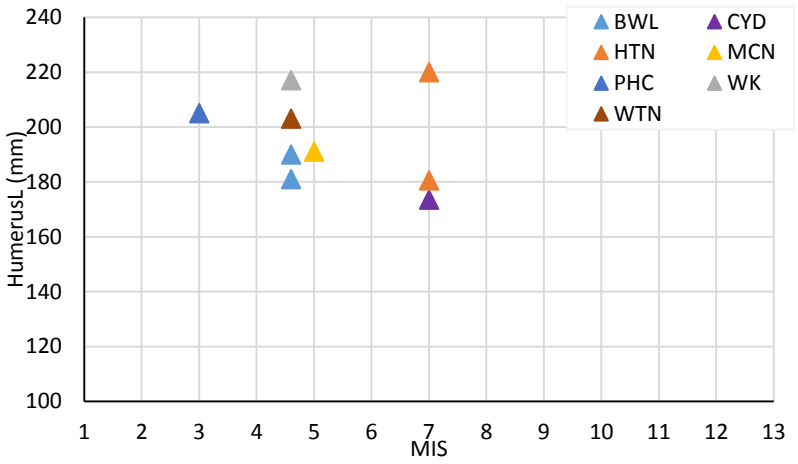


Figure 5.57. Greatest length humerus in *C. lupus* from Britain. CYD: Crayford, HTN: Hutton Cave, MCN: Michin Hole, WK: Windy Knoll, WTN: Wretton, BWL: Banwell Bone Cave, WK: Windy Knoll, PHC: Pin Hole Cave.

C. lupus humerus length varies within each age group and within each site (e.g. Hutton Cave). The shortest length is at Crayford (MIS 7).

Complete femora were few, with large variation in length indicated at Banwell Bone Cave, and the longest length also present in MIS 5a at Windy Knoll (Figure 6.58). Nonetheless, the Hutton individual (MIS 7) is of similar length to an individual at Banwell.

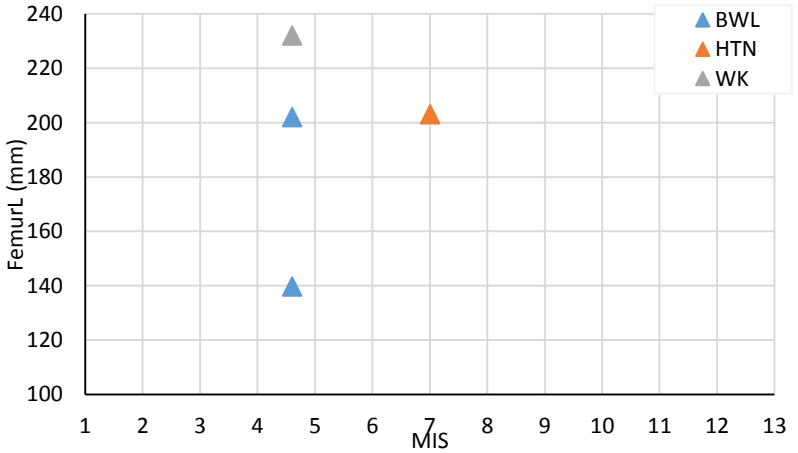


Figure 5.58. Greatest length femur in *C. lupus* from Britain. HTN: Hutton Cave, BWL: Banwell Bone Cave, WK: Windy Knoll.

Few complete tibia were also recorded. Lengths were overall similar, with the longest tibial lengths present at Windy Knoll (MIS 5a) (Figure 5.59).

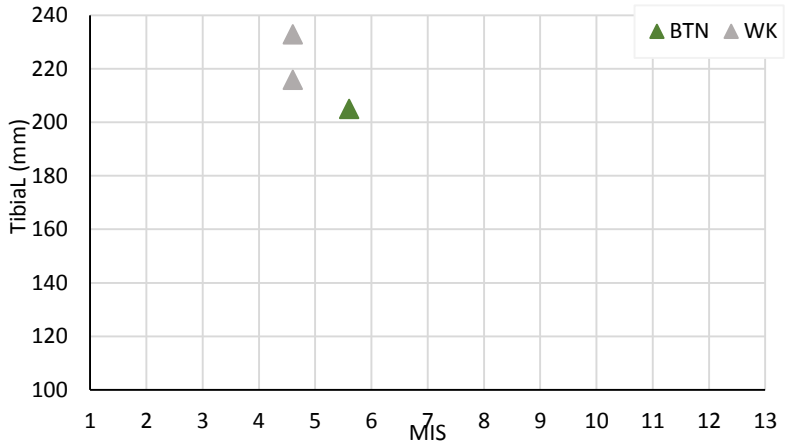


Figure 5.59. Greatest length tibia in *C. lupus* from Britain. BTN: Barrington, WK: Windy Knoll.

5.1.7. Comparison of *C. mosbachensis* m1L

The m1L of *C. mosbachensis* from sites recorded in this research was compared to published values from the smaller, southern European *Canis* aff. *arnensis* from Petralona, Greece and l'Escale, France (Kurtén and Poulianos, 1977) (Figure 5.60). *C. mosbachensis* was considered to be a northern European variant of *C.* aff. a*rnensis* by Rook and Torre (1996b) and comparisons were therefore made of m1L to explore any potential differences between the two canids, as well as to see how they compared against *C. mosbachensis*' apparent forerunner, *C. etruscus*.

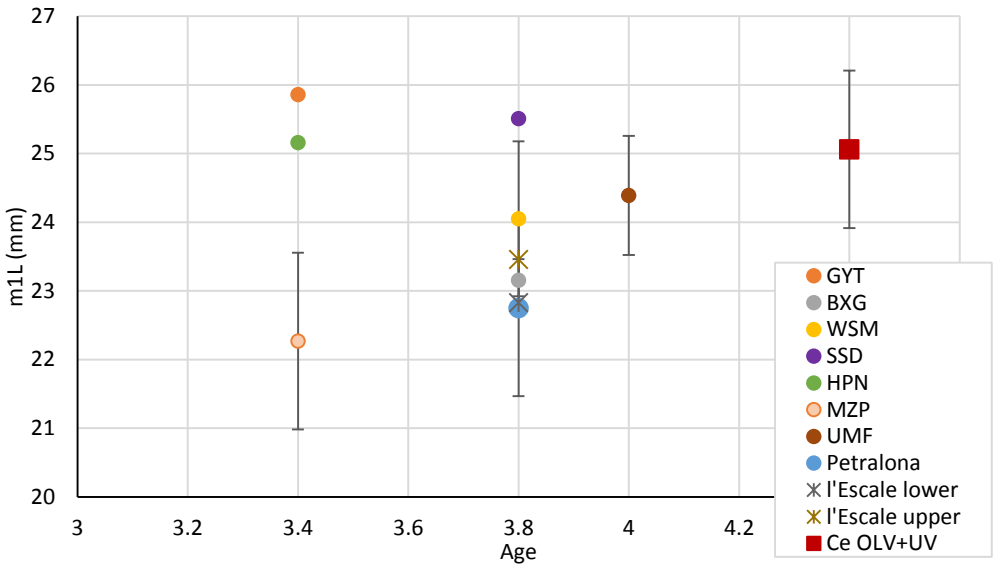


Figure 5.60. Comparison of m1L in *C. mosbachensis* from material analysed in this research with published measurement values from Petralona Cave, Greece and L'Escale, France (both from Kurten and Poulianos, 1977). *C. etruscus* from Olivola and Upper Valdarno included for comparison. Sites: GYT Grays Thurrock; BXG Boxgrove; WSM Westbury sub Mendip; SSD Sidestrand; HPN Heppenloch; MZP Monte Zoppega; UMF Untermassfeld; Ce UV+OLV *C. etruscus* from Olivola and Upper Valdarno.

C. mosbachensis from Grays Thurrock, Heppenloch, Sidestrand, Westbury sub Mendip and Untermassfeld were similar in m1L to *C. etruscus* from Olivola and the Upper Valdarno. Monte Zoppega, Petralona, l'Escale and Boxgrove are more similar in relative shortness of m1L. Westbury overlaps in its variation with Boxgrove, Petralona and l'Escale.

5.2. Body mass

5.2.1 Scaling of predictor measurements with body mass

Least squares regression was undertaken to evaluate scaling relationships in the predictor measurements (m1L, P4L) using the modern canid dataset of 28 species (see Chapter 4), together with published measurements (see Table 5.17).

5.2.1.1. Least squares regression of m1L with body mass

5.2.1.1.1. Regression 1

A Least Squares regression of log_{10} transformed m1L and body mass was performed using the modern canid dataset (regression 1). The results are shown in Table 5.18, and illustrated in Figure 5.61a.

Regres. no.	Measure	n species	y-intercept (a)	Allometric coefficient (b)	r^2	SEE	SE_b	*t*	*p*
1	m1L	28	0.834	0.386	0.734	0.091	0.046	8.462	0.0001
2	m1L	26	0.873	0.364	0.921	0.043	0.022	16.728	0.0001
3	**m1L**	**25**	**0.857**	**0.379**	**0.937**	**0.039**	**0.020**	**18.552**	**0.0001**

Table 5.18. Results of least squares regression for m1L on body mass. Final regression in bold.

Regression 1 was found as significant by ANOVA ($F_{1, 27}$ = 71.611, *p*=0.0001), with a highly significant slope (*b*) (t=8.462, *p*=0.0001). The moderately high r^2 indicates comparatively high correlation between m1L and body mass, as does the low SEE (Table 5.18).

Species	Sex	Ave BM (Kg)	Log_{10} Bm	m1L (mm)	n	Log_{10} m1L	P4L (mm)	n	Log_{10} P4L	Sources for BM
Canis adustus	All	10.8	1.033	16.85	10	1.227	15.47	10	1.189	8, 19
	Male	9.4	0.973	16.87	5	1.227	15.82	5	1.199	4
	Female	8.3	0.919	16.83	5	1.226	15.12	5	1.180	4
Canis aureus	All	11	1.041	17.75	10	1.249	16.03	10	1.205	8, 30
	Male	8.8	0.944	17.8	5	1.250	16.29	5	1.212	23
	Female	8.15	0.911	17.69	5	1.248	15.76	5	1.198	23
*Canis latrans**	All	14.25	1.154	21.2	10	1.326	18.9	10	1.276	6, 30
	Male	14	1.146	21.4	5	1.330	18.8	5	1.274	6
	Female	12.5	1.097	21	5	1.322	19	5	1.279	6
Canis lupus	All	41.33	1.616	29.2	10	1.465	26.61	10	1.425	1, 19, 31
	Male	46.67	1.669	30.46	5	1.484	27.91	5	1.446	1, 19
	Female	38.11	1.581	27.93	5	1.446	25.3	5	1.403	1, 18, 19
Canis mesomelas	All	8.75	0.942	18.66	10	1.271	17.3	10	1.238	8, 19
	Male	8.25	0.916	19.03	5	1.279	17.89	5	1.253	28
	Female	7.25	0.860	18.28	5	1.262	16.71	5	1.223	18, 28
Canis simensis	All	15.6	1.193	18.15	4	1.259	15.82	4	1.199	8, 37
	Male	16.2	1.210	19.23	1	1.284	16.28	1	1.212	37

	Female	13.65	1.135	17.78	3	1.250	15.66	3	1.195	18, 37
*Chrysocyon brachyurus**	All	23	1.362	22.9	6	1.360	18.1	4	1.258	15, 30, 33
Cuon alpinus	All	16.93	1.229	21.59	10	1.334	20.56	10	1.313	6, 19, 30
	Male	17.5	1.243	21.65	5	1.335	20.82	5	1.318	11
	Female	11.5	1.061	21.53	5	1.333	20.3	5	1.307	11, 18
Lycaon pictus	All	24.83	1.395	24.72	10	1.393	21.34	10	1.329	6, 8, 30
	Male	28	1.447	25.01	5	1.398	21.5	5	1.332	40
	Female	24.5	1.389	24.44	5	1.388	21.19	5	1.326	18, 40
*Speothos venaticus**	All	5.75	0.760	13.4	7	1.127	12.4	7	1.093	14, 30
*Alopex Lagopus**	All	3.53	0.548	13.05	10	1.116	11.7	10	1.068	7, 10
	Male	3.94	0.595	13.5	5	1.130	12.1	5	1.083	5, 34
	Female	3.35	0.525	12.6	5	1.100	11.3	5	1.053	5, 34
*Cerdocyon thous**	All	5.95	0.775	14.25	6	1.154	12.05	6	1.081	30, 33
*Pseudalopex culpaeus**	All	8.1	0.908	16.2	6	1.210	15.4	6	1.188	24, 30
	Male	8.5	0.929	16.5	3	1.217	15.4	3	1.188	24
	Female	6.58	0.818	15.9	3	1.201	15.4	3	1.188	24
*Pseudalopex griseus**	All	3.65	0.562	13.55	10	1.132	12.1	10	1.083	20, 30
	Male	4	0.602	13.8	5	1.140	12.3	5	1.090	20
	Female	3.1	0.491	13.3	5	1.124	11.9	5	1.076	20

*Pseudalopex gymnocercus**	All	5	0.699	14.05	5	1.148	12.6	5	1.100	29, 30
	Male	5.47	0.738	14.5	2	1.161	13.2	2	1.121	29
	Female	4.5	0.653	13.6	3	1.134	12	3	1.079	29
*Pseudalopex sechurae**	All	3.6	0.556	11.45	5	1.059	9.7	5	0.987	2, 30
*Pseudalopex vetulus**	All	3.38	0.529	9.6	6	0.982	7.9	6	0.898	13, 30
	Male	3.3	0.519	9.4	4	0.973	7.9	4	0.898	13
	Female	3.4	0.531	9.8	2	0.991	7.9	2	0.898	13
*Urocyon cinereoargenteus**	All	4.45	0.648	11.15	10	1.047	9.1	10	0.959	16, 30
	Male	4	0.602	11.3	5	1.053	9.4	5	0.973	17
	Female	3.3	0.519	11	5	1.041	8.8	5	0.944	17
*Urocyon littoralis**	All	1.9	0.279	8.5	10	0.929	7.9	10	0.898	30, 35
	Male	2	0.301	7.7	5	0.886	7.9	5	0.898	35
	Female	1.8	0.255	9.3	5	0.968	7.9	5	0.898	35
*Vulpes bengalensis**	All	2.5	0.398	10.4	7	1.017	8.35	7	0.922	30
	Male	2.95	0.470	10.8	5	1.033	8.9	5	0.949	25
	Female	1.8	0.255	10	2	1.000	7.8	2	0.892	25
*Vulpes chama**	All	2.88	0.459	11.05	10	1.043	9.2	10	0.964	30, 38
	Male	2.8	0.447	11.1	5	1.045	9.3	5	0.968	38
	Female	2.5	0.398	11	5	1.041	9.1	5	0.959	38
*Vulpes macrotis**	All	2.11	0.324	11.15	10	1.047	9.25	10	0.966	27, 30
	Male	2.29	0.360	11	5	1.041	9.2	5	0.964	27
	Female	1.9	0.279	11.3	5	1.053	9.3	5	0.968	27
*Vulpes pallida**	All	2.8	0.447	9.05	7	0.957	7.9	7	0.898	30, 36
*Vulpes rueppelli**	All	1.66	0.220	11.15	10	1.047	9.75	10	0.989	12, 30
	Male	1.68	0.225	11.1	5	1.045	9.6	5	0.982	12

	Female	1.54	0.188	11.2	5	1.049	9.9	5	0.996	12
Vulpes vulpes	All	6.83	0.834	15.2	4	1.182	14.66	4	1.166	9, 21, 22
	Male	5.96	0.775	15.08	2	1.178	14.95	2	1.175	7, 22
	Female	4.86	0.687	15.33	2	1.186	14.37	2	1.157	7, 22
*Vulpes zerda**	All	1.23	0.090	7.75	7	0.889	7.05	7	0.848	3, 30
*Nyctereutes procyonoides**	All	4.04	0.606	6.43	6	0.808	9.35	6	0.971	30, 39
*Otocyon megalotis**	All	4.18	0.621	5.95	9	0.775	5.2	9	0.716	26, 30
	Male	4	0.602	5.9	5	0.771	5.1	5	0.708	32
	Female	4.1	0.613	6	4	0.778	5.3	4	0.724	32

Table 5.17. The body mass of recent canids used in scaling and body mass reconstruction. Mean body mass with m1L and P4L (mm) shown. Means of body mass data calculated from literature for both sexes, and separate sexes where possible, where $\log_{10}$ transformations shown. *n*: number of individuals. *indicates measurement data from Palmqvist et al. (2002). Sources for body mass: 1). Body weight data from NRM; 2). Asa and Cossios (2004), 3). Asa et al. (2004), 4). Atkinson and Loveridge (2004), 5). Ballard et al. (2000), 6). Bekoff (1977), 7). Bueler (1973), 8). Caro and Stoner (2003), 9). Cavallini (1995), 10). Chesemore (1975), 11). Cohen (1978), 12). Cuzin and Lenain (2004), 13). Dalponte and Courtneay (2004), 14). de Mello Beisiegel and Zuercher (2005), 15). Dietz (1985), 16). Fritzell and Haroldson (1982), 17). Fuller and Cypher (2004), 18). Geffen et al. (1996), 19). Gittleman (1986), 20). Gonzalez del Solar and Rau (2004), 21). Haltenoth and Roth (1968), 22). Hattingh (1956), 23). Jhala and Moehlman (2004), 24). Jimenez and Novaro (2004), 25). Johnsingh and Jhala (2004), 26). Kingdon (1977), 27). List and Cypher (2004), 28). Loveridge and Nel (2004), 29). Lucherini et al. (2004), 30). Macdonald (2009), 31). Mech (1974), 32). Nel and Maas (2004), 33). Nowak (1999), 34). Prestrud and Nilssen (1995), 35). Roemer et al. (2004), 36). Sillero-Zubiri (2004), 37). Sillero-Zubiri and Gottelli (1994), 38). Stuart and Stuart (2004), 39). Ward and Wurster-Hill (1990), 40). Woodroffe et al. (2004).

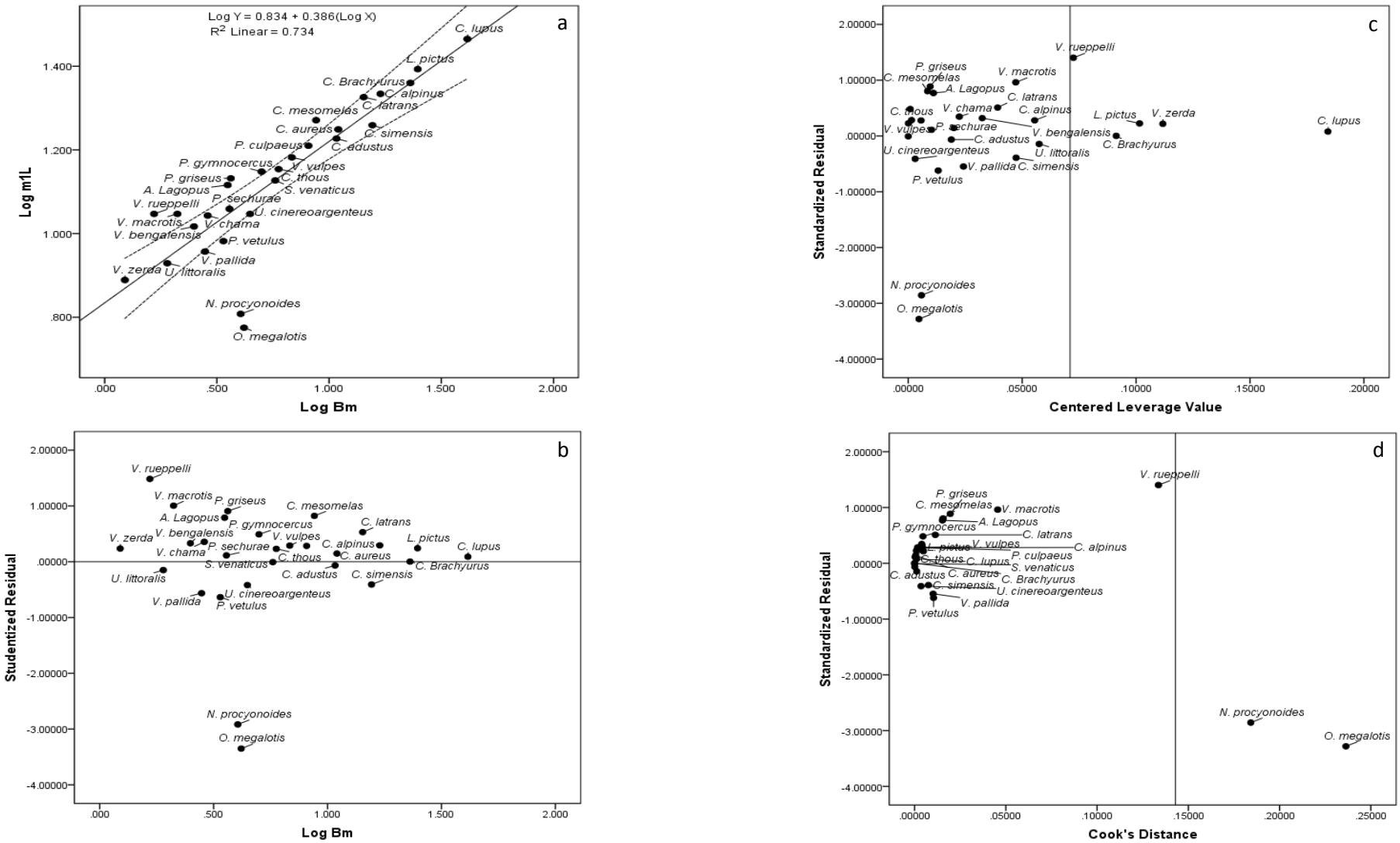


Figure 5.61. Least squares regression of m1L on body mass (regression 1). a). Regression line, b). Studentised residuals plotted with $\log_{10}$ body mass, c). Standardised residuals plotted with leverage, line indicating high leverage >0.071, d). Standardised residuals plotted with Cook's D, line indicating high influence >0.143.

Examination of Figure 5.61a indicates a strong positively linear correlation between m1L and body mass, which was found to be significant by Pearson product moment correlation (Pearson correlation r_{28} = 0.857, *p*=0.0001). Both *N. procyonoides* and *O. megalotis* are outliers, plotting outside the regression line and 95% confidence interval area (Figure 5.61a) within which the remaining data were explained. To assess these outliers, the studentised residuals were plotted against the body mass (Figure 5.61b). Both *N. procyonoides* and *O. megalotis* have high residual values >2 (-2.917, -3.350 respectively), indicative of outliers.

The leverage and influence of the species were assessed, to determine whether undue influence or leverage was being exerted over the model. Leverage is estimated by 2*p*/*n* where p is the number of predictor variables (in this case 1), and *n* is the sample size (in this case 28). Thus, species with leverage > 0.071 are considered to have high leverage in the regression (Figure 5.61c). Both *N. procyonoides* and *O. megalotis* have low leverage, whereas C*. lupus, V. zerda, L. pictus* and *C. bracyurus* have high leverage. Although high leverage points can cause distortion in the regression model, these species were not identified as outliers and plot close to the regression line. Low leverage outliers are less distorted, although their associated large residuals inflate SEE and decrease r^2. However, points with high leverage are not necessarily outliers, especially if they plot close to the regression line (Figure 5.61a); influence must therefore to be assessed.

The level of Influence (Cook's D) is estimated by *Di* = >4/*n* where n is sample size (in this case 28). Thus, species with influence > 0.143 are considered to have high influence (Figure 5.61d). Both *N. procyonoides* and *O. megalotis* have high influence. In contrast, species with high leverage do not have high influence. High leverage species that were not identified as outliers and had low influence were retained in the analysis. However, both *N. procyonoides* and *O. megalotis* were removed as outliers with both low leverage and high influence.

As a final test, the standardised residuals from the regression were checked for outliers and normality by Q-Q plots and Shapiro-Wilk tests. As expected, both *N. procyonoides* and *O. megalotis* were identified as outliers, and the residuals as non-normally distributed (Shapiro-Wilk test: W_{28} = 0.746, *p*=0.0001).

5.2.1.1.2. Regression 2

After removal of *N. procyonoides* and *O. megalotis*, m1L was regressed on body mass using the revised dataset of 26 species (Table 5.18 and Figure 5.62a). Regression 2 was found to be significant by ANOVA ($F_{1, 25}$ = 279.827, *p*=0.0001), with a highly significant slope (*b*) (t=16.728, *p*=0.0001). The removal of outliers has increased the r^2, and decreased the SEE (Table 5.18). Figure 5.62a reveals a strong positively linear correlation between m1L and body mass, with a significant Pearson correlation (r_{27} = 0.960, *p*=0.0001). *V. rueppelli* was identified as an outlier in the studentised residuals (Figure 6.62b) with a value of 2.315.

Leverage was once more examined, with values >0.077 considered as having high leverage (Figure 5.62c). Once again, C*. lupus, V. zerda, L. pictus* and *C. brachyurus* have high leverage, however they plot close to the regression line and are not therefore considered to be outliers. Influence was also examined, with values >0.154 considered as having high influence (Figure 5.62d). The only highly influential species was identified as *V. rueppelli* (0.348).

The standardised residuals were again checked for outliers and normality by Q-Q plots and Shapiro-Wilk test. As expected, *V. rueppelli* was identified as an outlier, although distribution was now found to be not non-normal (Shapiro-Wilk W_{26} =0.975, *p*=0.752). Following regression 1, *V. rueppelli* was removed from the analysis for being an outlier with high influence.

5.2.1.1.3. Regression 3

After removal of *N. procyonoides, O. megalotis* and *V. rueppelli*, m1L was regressed against body mass using the remaining 25 canid species dataset (Table 5.18 and Figure 5.63a). Regression 3 was found to be significant by ANOVA ($F_{1, 24}$ = 344.182, *p*=0.0001), with a highly significant slope (*b*) (t=18.552, *p*=0.0001). The removal of the outliers has increased the r^2 and decreased the SEE. No further outliers were identified (Figure 5.63b), although *V. vetulus* has a studentised residual value of 2.003.

Although no additional species were identified as outliers, leverage and influence were still assessed. High leverage was indicated by values >0.08 (Figure 5.63c). Once again C*. lupus, V. zerda, L. pictus* and *C. brachyurus* had high leverage, although they continue to plot close to the regression line. High influence was indicated by values >0.16 (Figure 5.63d). *V. macrotis* was indicating as having high influence. However, as no species were identified as outliers, high leverage and high influence are irrelevant. A Shapiro-Wilk test of the residuals found them to be not non-normally distributed (W_{25} = 0.961, *p*=0.437).

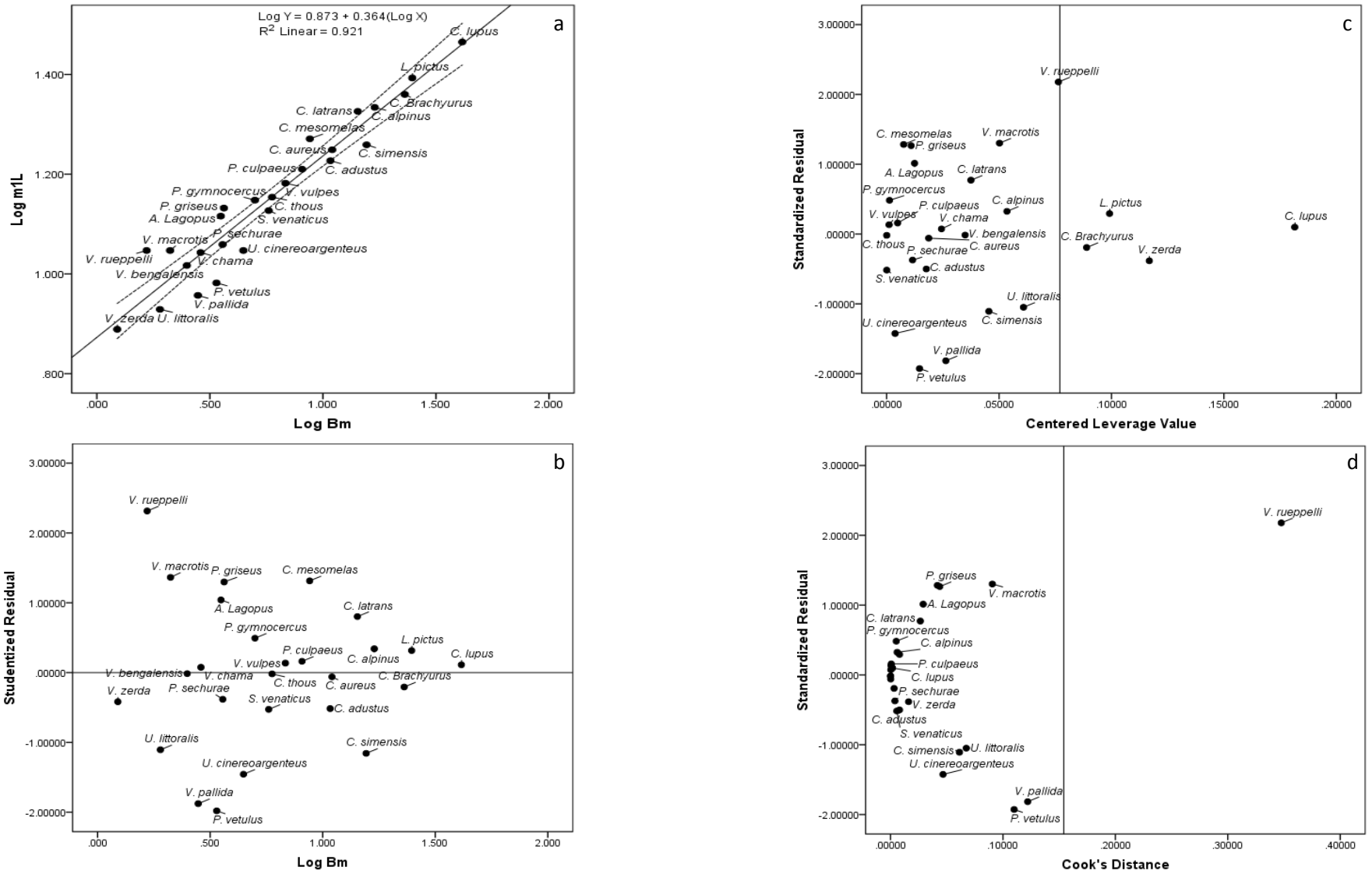


Figure 5.62. Least squares regression of m1L on body mass (regression 2). a). Regression line, b). Studentised residuals plotted with $\log_{10}$ body mass, c). Standardised residuals plotted with leverage, line indicating high leverage >0.077, d). Standardised residuals plotted with Cook's D, line indicating high influence >0.154.

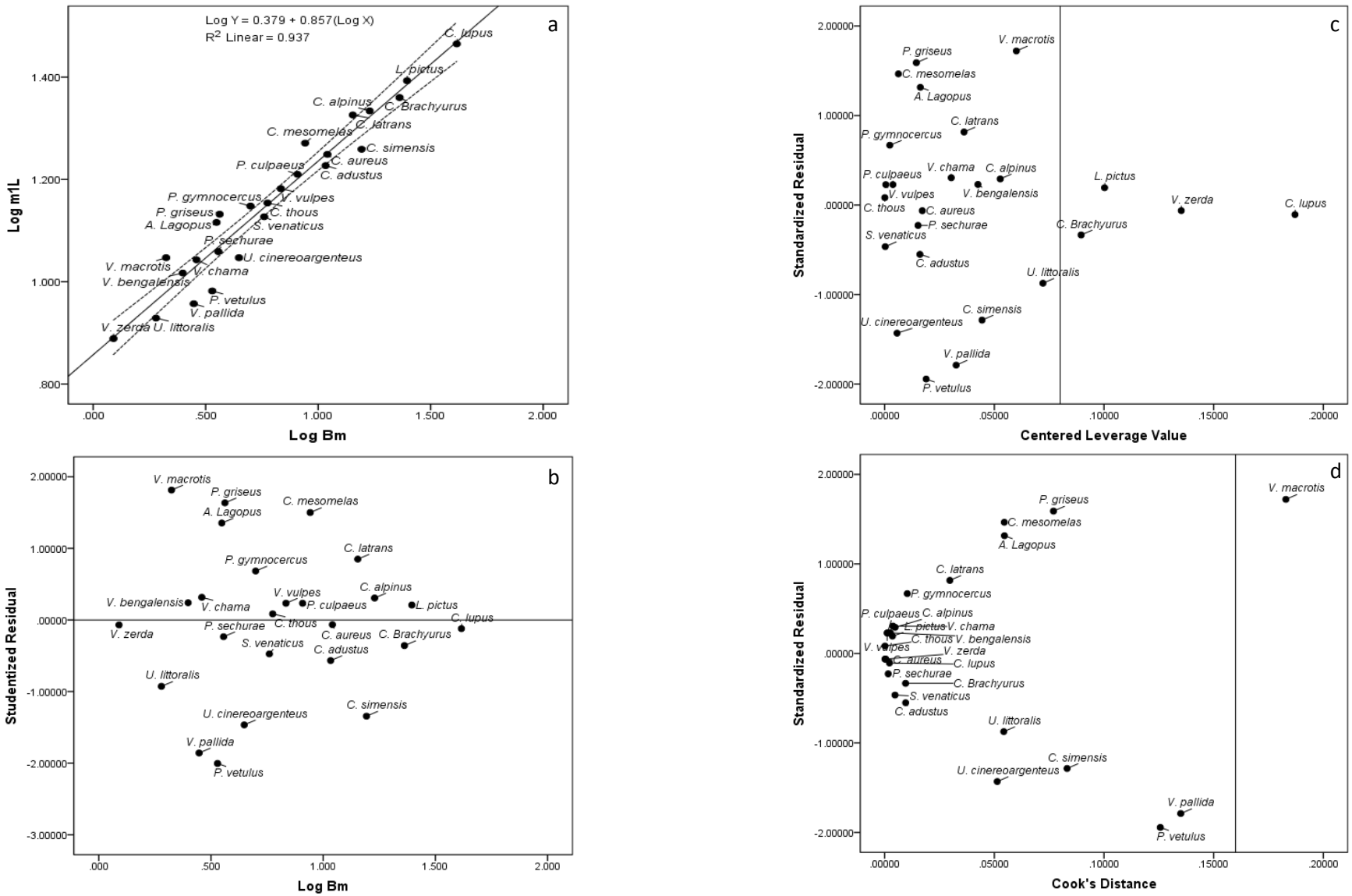


Figure 5.63. Least squares regression of m1L on body mass (regression 3). a). Regression line, b). Studentised residuals plotted with $\log_{10}$ body mass, c). Standardised residuals plotted with leverage, line indicating high leverage >0.08, d). Standardised residuals plotted with Cook's D, line indicating high influence >0.16.

5.2.1.2. Scaling of m1L with body mass

Regression 3 provided the best regression model for exploring scaling between m1L and body mass. The allometric coefficient for m1L (*b* = 0.379) is higher than the expected slope of geometric similarity (*b* = 0.333), indicating that m1L is slightly positively allometric with body mass. However, the presence of significant difference between these slopes will be explored in 5.2.1.5.

5.2.1.3. Least squares regression of P4L with body mass.

5.2.1.3.1. Regression 1

The results of the regression of P4L on body mass are shown in Table 5.19, and illustrated in Figure 5.64a.

Regres. no.	Measure	n species	y-intercept (a)	Allometric coefficient (b)	r^2	SEE	SE_b	t	*p*
1	P4L	28	0.786	0.388	0.777	0.081	0.041	9.511	0.0001
2	**P4L**	**27**	**0.806**	**0.376**	**0.887**	**0.054**	**0.027**	**13.981**	**0.0001**

Table 5.19. Results from least squares regression of P4L and body mass. Final regression in bold.

Regression 1 was found to be significant by ANOVA ($F_{1, 27}$ = 90.454, *p*=0.0001), with a highly significant slope (*b*) (t=9.511, *p*=0.0001). The moderately high r^2 indicates moderately high correlation between m1L and body mass, as does the low SEE (Table 5.19). Figure 5.64a reveals a strong positively linear correlation between P4L and body mass, with a significant Pearson correlation (r_{28} = 0.881, *p*=0.0001).

This regression placed *O. megalotis* as an outlier from the regression line (Figure 5.64a), and revealed a large studentised residual of -3.891 (Figure 5.64b). *C. lupus, V. zerda, L. pictus, C. brachyurus* and *V. rueppelli* have high leverage (>0.071) (Figure 5.64c). Although *V. rueppelli* has only slightly elevated leverage, and was not identified as an outlier in the residuals, this species plots the furthest from the regression line. The remaining canids all plot close to the regression line and are therefore not considered as outliers, albeit having high leverage.

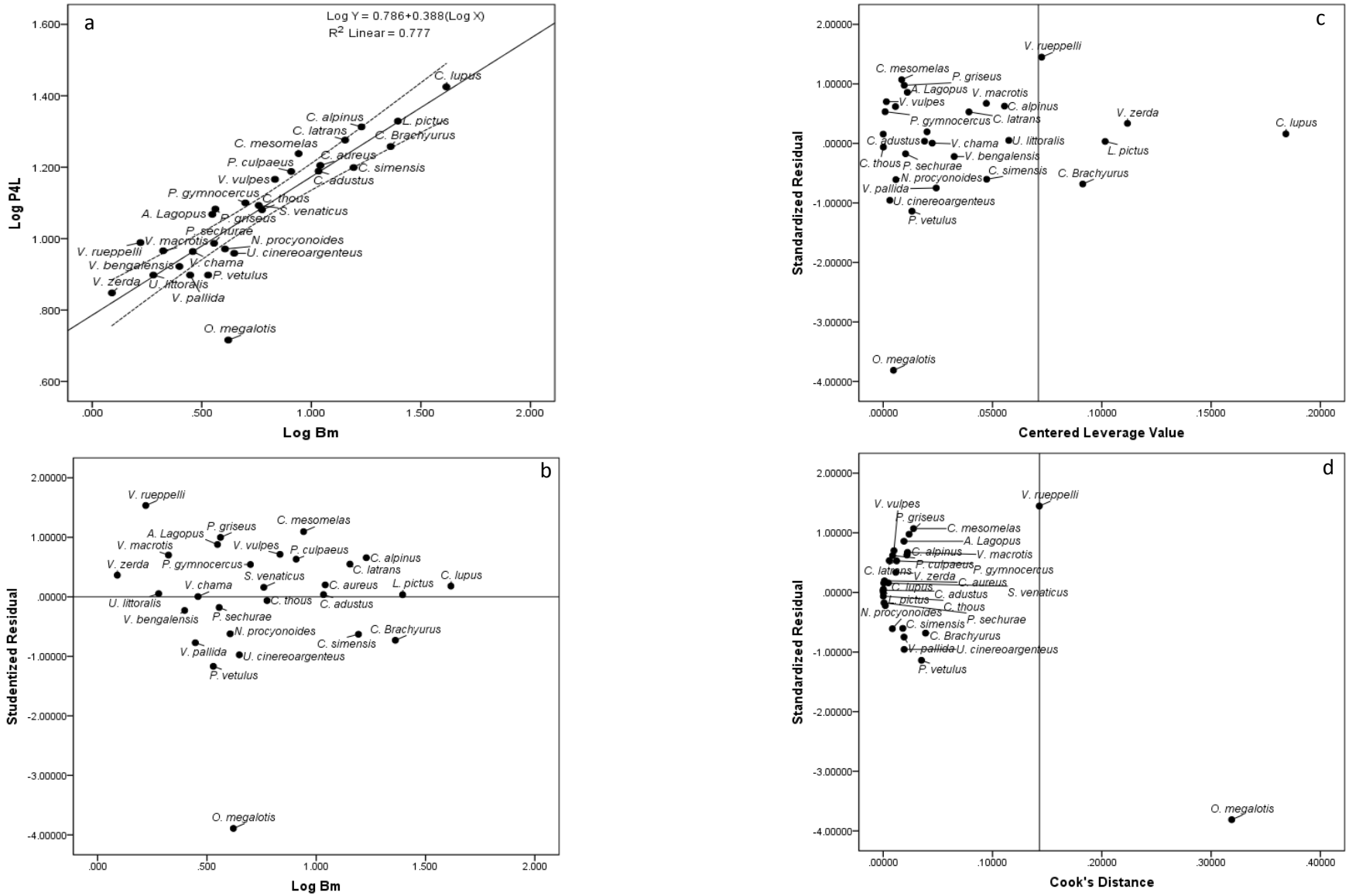


Figure 5.64. Least squares regression of P4L on body mass (regression 1). a). Regression line, b). Studentised residuals plotted with $\log_{10}$ body mass, c). Standardised residuals plotted with leverage, line indicating high leverage >0.071, d). Standardised residuals plotted with Cook's D, line indicating high influence >0.143.

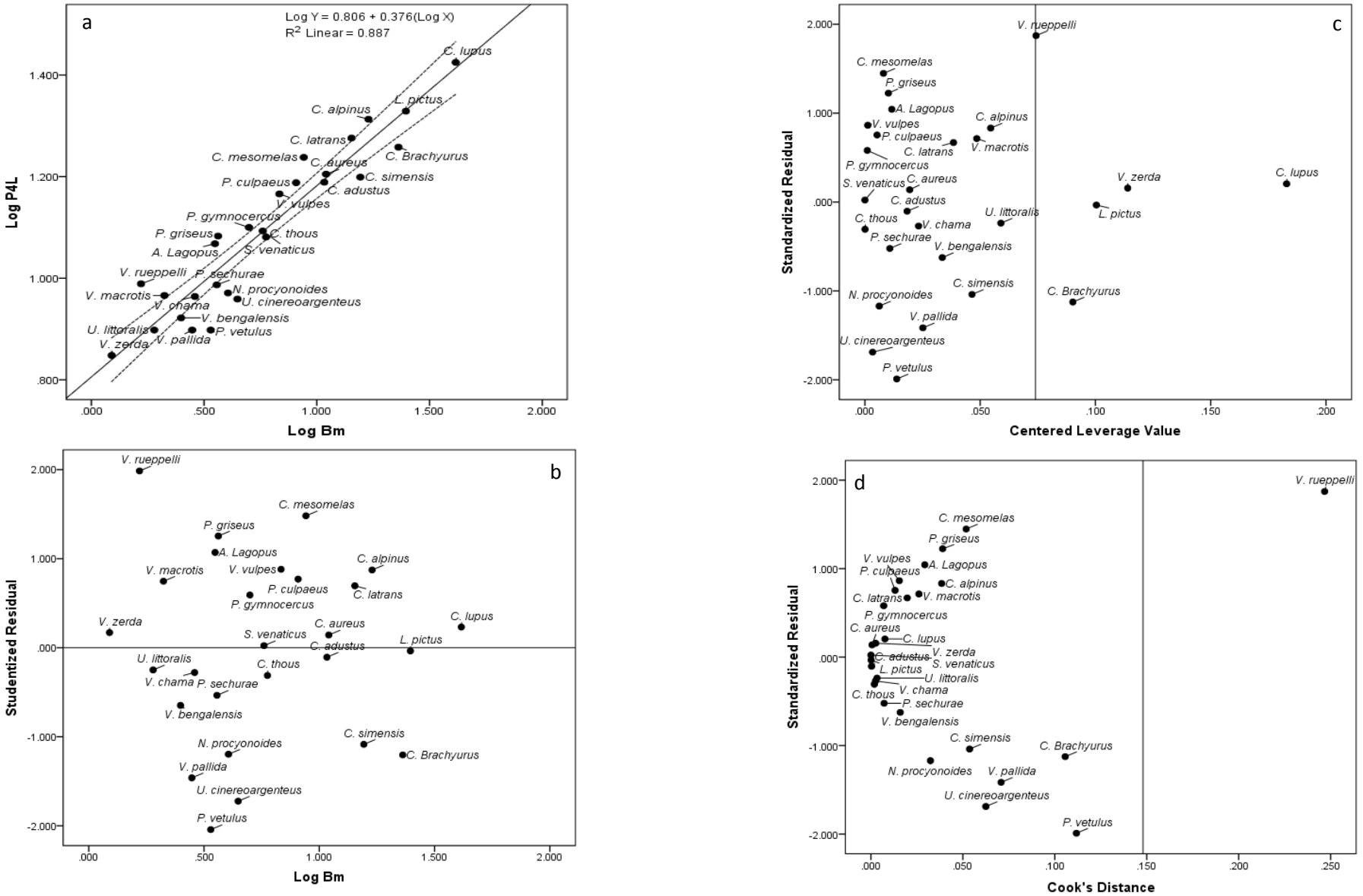


Figure 5.65. Least squares regression of P4L on body mass (regression 2). a). Regression line, b). Studentised residuals plotted with $\log_{10}$ body mass, c). Standardised residuals plotted with leverage, line indicating high leverage >0.074, d). Standardised residuals plotted with Cook's D, line indicating high influence >0.148.

High influence (>0.143) was revealed for *O. megalotis* (Figure 5.64d), with *V. rueppelli* on the cut off for this measure. The residuals were checked for outliers and normality by Q-Q plots and Shapiro-Wilk test. As expected, *O. megalotis* was identified as an outlier and found to be not normally distributed (Shapiro-Wilk test W_{28} = 0.824, *p*=0.0001). This species has low leverage but high influence and was subsequently removed from the regression analysis.

5.2.1.3.2. Regression 2

With the removal of *O. megalotis*, P4L was regressed on body mass using the 27 species dataset (Table 5.19 and Figure 5.65). The removal of the outlier increased the r^2 and decreased SEE. Although no points are exceptionally far from the regression line (Figure 5.65a), *P. vetulus* has a studentised residual of -2.043 (Figure 5.65b), which is close to the high residual cut off of 2.00. Although there is only one putative outlier, leverage and influence were still assessed. High leverage species (values >0.074) (Figure 5.65c) include *C. lupus, V. zerda, L. pictus, C. brachyurus,* with *V. rueppelli* on the cut-off at 0.074. None of these species were identified as outliers. *C. lupus, V. zerda, L. pictus* all plot close to the regression line, and although they have high leverage, they are not outliers. *V. rueppelli* lies slightly further off the regression line but was not identified as an outlier.

V. ruepelli was identified as having high influence (>0.148) (Figure 5.65d). The residuals were also checked for outliers and normality by Q-Q plots and Shapiro-Wilk test. No species were identified as outliers, and the residuals were found as not non-normally distributed (Shapiro-Wilk test W_{27} = 0.982, *p*=0.907). Although *P. vetulus* was found as a potential outlier, it has neither high leverage nor influence and was therefore retained in the analysis. *V. rueppelli* was lay at the limit of high leverage and with high influence. However, it was not found as an outlier and was not removed from the analysis.

5.2.1.4. Scaling of P4L with body mass

P4L also had a strong positive linear relationship with body mass, with Regression 2 the best identified model. The allometric coefficient for P4L (*b* = 0.376) is higher than the expected slope of geometric similarity (*b* = 0.333), indicating that P4L (like m1L) is also slightly positively allometric with regards to body mass. Thus, as body mass increases, P4L

increases at a slightly faster rate. The presence of significant differences between these slopes will be explored in the following section.

5.2.1.5. Testing the significance of the allometric coefficient (*b*)

To test whether the allometric coefficient (*b*) for both regressions using m1L and P4L is significantly different from the expected slope of geometric similarity, a *t* test was employed with the H_0: $\beta = \beta_{0.333}$, that the slopes (the allometric coefficient) of the regressions equal that of geometric similarity. Thus for the chosen m1L regression, in order to reject the H_0 (that the slope is equal to that of geometric similarity) the following comparison for the *t* test is used: $t \geq t_{0.05,\,(1),\,23.}$ Hence, the calculated *t* value is compared to the critical value of *t*, which is defined as: $t_{0.05,\,(1),\,23} = 1.7139$, where $\alpha = 0.05$, d.f. = n – 2.

In order to calculate t for comparison, the following equation outlined by Zar (2010) is used:

$$t = \frac{b - \beta_{0.333}}{SE_b}$$

Where *b* = allometric coefficient (slope), $\beta_{0.333}$ = geometric similarity, SEb = standard error of slope. Thus for m1L: *b* = 0.379, SE_b = 0.020, n=25 (d.f. = 23) (information from Table 5.18).

Hence, calculated $t = 2.300 > t_{0.05,\,(1),\,23}$ (1.7139), which is greater than the critical value of t, and thus rejects the H_0, indicating significant differences present between the allometric coefficient for m1L and the expected slope of geometric similarity. In light of this, the slight positive allometry found in m1L is statistically different from that of geometric similarity.

The same test was applied for P4L. Thus, based on the same comparison for the t test whereby $t \geq t_{0.05,\,(1),\,25}$, the critical value of t was defined as: $t_{0.05,\,(1),\,25} = 1.7081$, where $\alpha = 0.05$, d. f. = n – 2. The subsequent calculation of t itself (using the main equation above, and based on *b* = 0.376, SEb = 0.027, n=27 (d.f. = 25) [(information from Table 5.19], was found to be $t = 1.593 < t_{0.05,\,(1),\,25}$ (1.7081). Thus calculated t is therefore less than the critical value of t, which keeps the H_0, indicating similarity between the allometric coefficient for P4L and the expected slope of geometric similarity.

Even though the allometric coefficient for P4L was actually >0.333 (the value for geometric similarity), the subsequent *t* test found no statistical difference between the two slopes, thus indicating that P4L scales with geometric similarity to body mass.

5.2.2. Creating the regression model for estimating body mass

Sections 5.1.4 and 5.2 reveal that m1L and P4L are both of low variability and are slightly positively allometric with body mass. Least squares regression was used to model the relationship between the known body mass of selected modern canids and carnassial tooth length (m1 and P4) after transformation (Log_{10}) of the variables. Body weight in modern canids was taken from the literature (see Chapter 4 for sources) and from records in the Naturhistoriska riksmuseet, Stockholm. Mean body weight was calculated from these sources for both sexes, and for males and females separately (Table 5.17). However, for some species separate sex body weight was not found in the literature. In light of this, the body weights of the combined sexes were used to create the predictive model. As sexual size dimorphism for in canids is considered to be low in comparison to other Families such as mustelids and felids (Gittleman and Van Valkenburgh, 1997), including body weights based on male and female data was therefore not considered problematic. Mean body weight, together with mean m1L and P4L for the canids is shown in Table 5.17.

As outlined in Chapter 4, the predictive power of the regressions was assessed by comparing the coefficient of determination (r^2), the standard error of estimate (SEE). The percent standard error of estimate (%SEE) and the percent prediction error (%PE) were calculated for the model. The predicted body masses for the Pleistocene canids was then de-transformed and a correction factor applied to remove logarithmic transformation bias, following Smith (1993).

5.2.2.1. Least squares regression of body mass on m1L

5.2.2.1.1. Regression 1

Least Squares regression of log_{10} transformed body mass on m1L was performed using the 28 canid species dataset (Table 5.20 and Figure 5.66), despite the identification of outliers in Section 5.2.1.1.

Regression number	Measure	n species	y-intercept (a)	slope (b)	r^2	SEE	*t*	*p*

1	m1L	28	-1.385	1.902	0.734	0.202	8.462	0.0001
2	m1L	26	-2.149	2.532	0.921	0.114	16.728	0.0001
3	**m1L**	**25**	**-2.073**	**2.476**	**0.937**	**0.100**	**18.552**	**0.0001**

Table 5.20. Results of least squares regression of body mass on m1L. Final regression in bold.

Regression 1 was found to be significant by ANOVA ($F_{1, 26}$ = 71.611, *p*=0.0001), highlighting the significant relationship between body mass and m1L. A *t*-test found the slope (*b*) highly significant (t=8.462, *p*=0.0001), thus indicating the regression line as highly significant. The high r^2 indicates a moderately high correlation between body mass and m1L, as does the low SEE (Table 5.20).

Figure 5.66a illustrates a strong positively linear correlation between body mass and m1L, with a significant Pearson correlation (r_{28} = 0.857, p=0.0001). Further examination of Figure 5.66a indicates *N. procyonoides* and *O. megalotis* (and possibly also *V. ruepelli*) as outliers from the regression line and the bulk of the explained data. Inspection of the studentised residuals (Figure 5.66b) indicates *N. procyonoides* and *O. megalotis* as outliers with values of 2.452 and 2.919 respectively. *V. rueppelli* is below the cut-off for residual outliers (>2.00) at -1.952.

As with the analysis of scaling, the residuals were examined for their leverage and influence. High leverage was indicated by values >0.071 (Figure 5.66c), identifying *O. megalotis, N. procyonoides, C. lupus* and *L. pictus* as having high leverage. High influence was indicated by values >0.143 (Figure 5.66d), identifying *N. procyonoides* and *O. megalotis* as having high influence, with *C. lupus* just on the cut-off (0.147).

The residuals were also checked for outliers and normality using Q-Q plot and Shapiro-Wilk test. As expected, *N. procyonoides* and *O. megalotis* were identified as outliers, although the residuals were found to be not non-normally distributed (Shapiro-Wilk test W_{28} = 0.952, *p*=0.226). As *N. procyonoides* and *O. megalotis* were identified as outliers, with both high leverage and influence, these species were removed from the regression model. Although *C. lupus* and *L. pictus* had high leverage, and *C. lupus* was on the cut-off for influence, they were not found to be outliers and were retained.

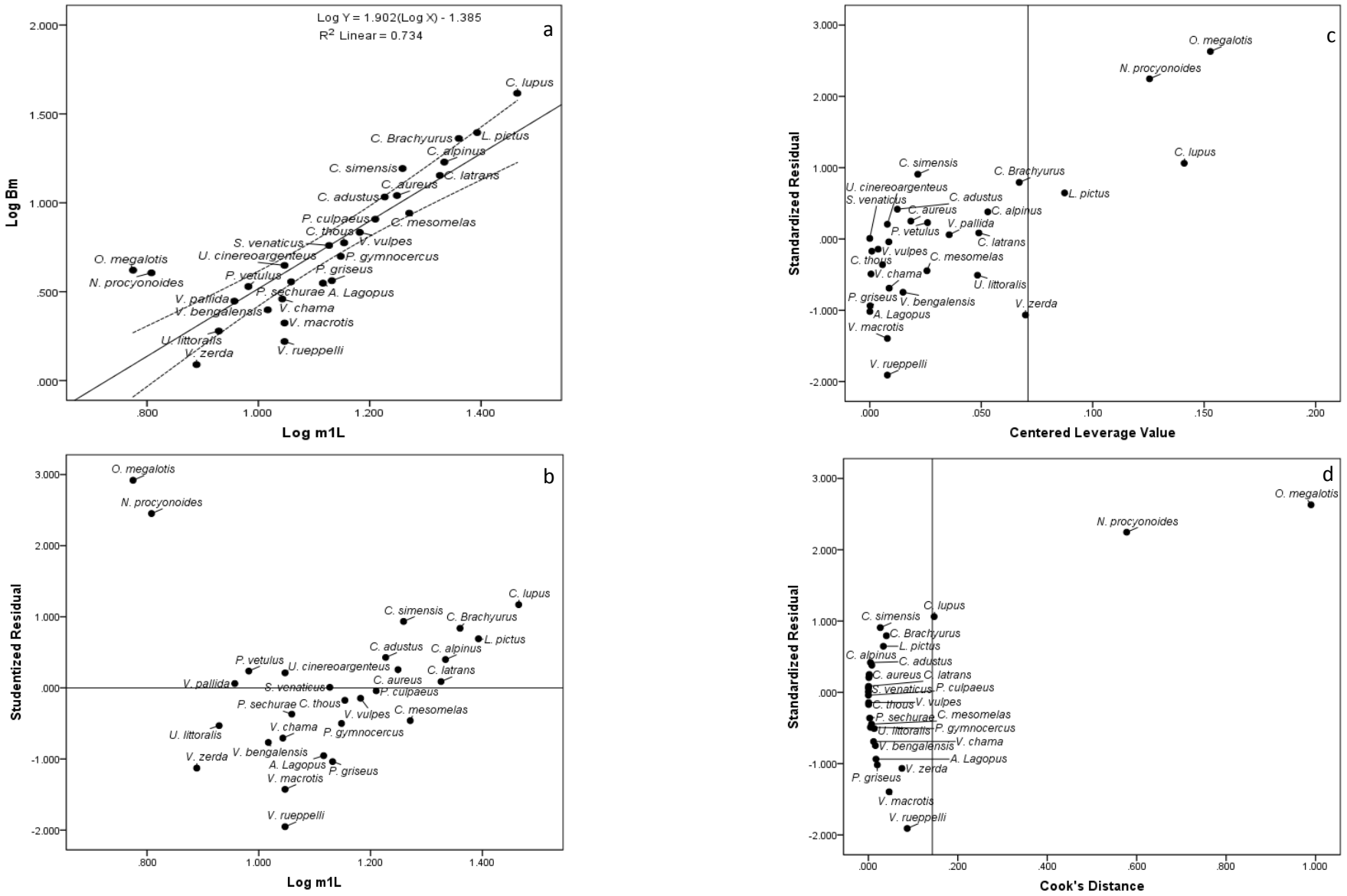


Figure 5.66. Least squares regression of body mass on m1L (regression 1). a). Regression line, b). Studentised residuals plotted with $\log_{10}$ m1L, c). Standardised residuals plotted with leverage, line indicating high leverage >0.071, d). Standardised residuals plotted with Cook's D, line indicating high influence >0.143.

5.2.2.1.2. Regression 2

With the removal of *N. procyonoides* and *O. megalotis,* body mass was regressed on m1L using the revised 26 species dataset (Table 5.20 and Figure 5.67).

Regression 2 was found as significant by ANOVA ($F_{1, 24}$ = 279.827, *p*=0.0001), highlighting the significance between body mass and m1L. A *t*-test found the slope (b) highly significant (t=16.728, *p*=0.0001), also indicating the regression line as highly significant. In comparison to regression 1, outlier removal has increased r^2 showing a much higher correlation between body mass and m1L, combined with a decreased SEE (Table 5.20).

A strong positively linear correlation between body mass and m1L is shown by Figure 5.67a, with a significant Pearson correlation (r_{26} = 0.960, *p*=0.0001). *V. rueppelli* lies furthest from the regression line and was identified as an outlier, with a high studentised residual value of -2.546 (Figure 5.67b). The residuals were further examined for leverage and influence. High leverage was indicated by >0.077 (Figure 5.67c). *C. lupus, V. zerda, L. pictus* and *U. littoralis* were identified as having high leverage but all plotted close to the regression line. High influence was indicated by >0.154 (Figure 5.67d). *V. rueppelli* was identified as having high influence, with both *P. vetulus* and *V. pallida* just below the cut-off of high influence.

Residuals were checked for outliers and normality using Q-Q plot and Shapiro-Wilk test. As expected *V. rueppelli* was identified as an outlier, although the residuals were found to be not non-normally distributed (Shapiro-Wilk test W_{26}=0.967, *p*=0.539). As an outlier with high influence, albeit low leverage, *V. rueppelli* was removed from the regression model.

5.2.2.1.3. Regression 3

With the removal of *N. procyonoides, O. megalotis* and *V. rueppelli*, body mass was regressed on m1L using the revised 25 species dataset (Table 5.20 and Figure 5.68).

The regression was found to be significant by ANOVA ($F_{1, 23}$ = 344.182, *p*=0.0001), highlighting the significance between body mass and m1L. A *t*-test found the slope (*b*) highly significant (t=18.552, *p*=0.0001), further indicating the significance of the regression line.

With the removal of the further species outlier, r^2 has increased slightly, indicating a higher correlation between body mass and m1L, whilst SEE has slightly decreased (Table 5.20).

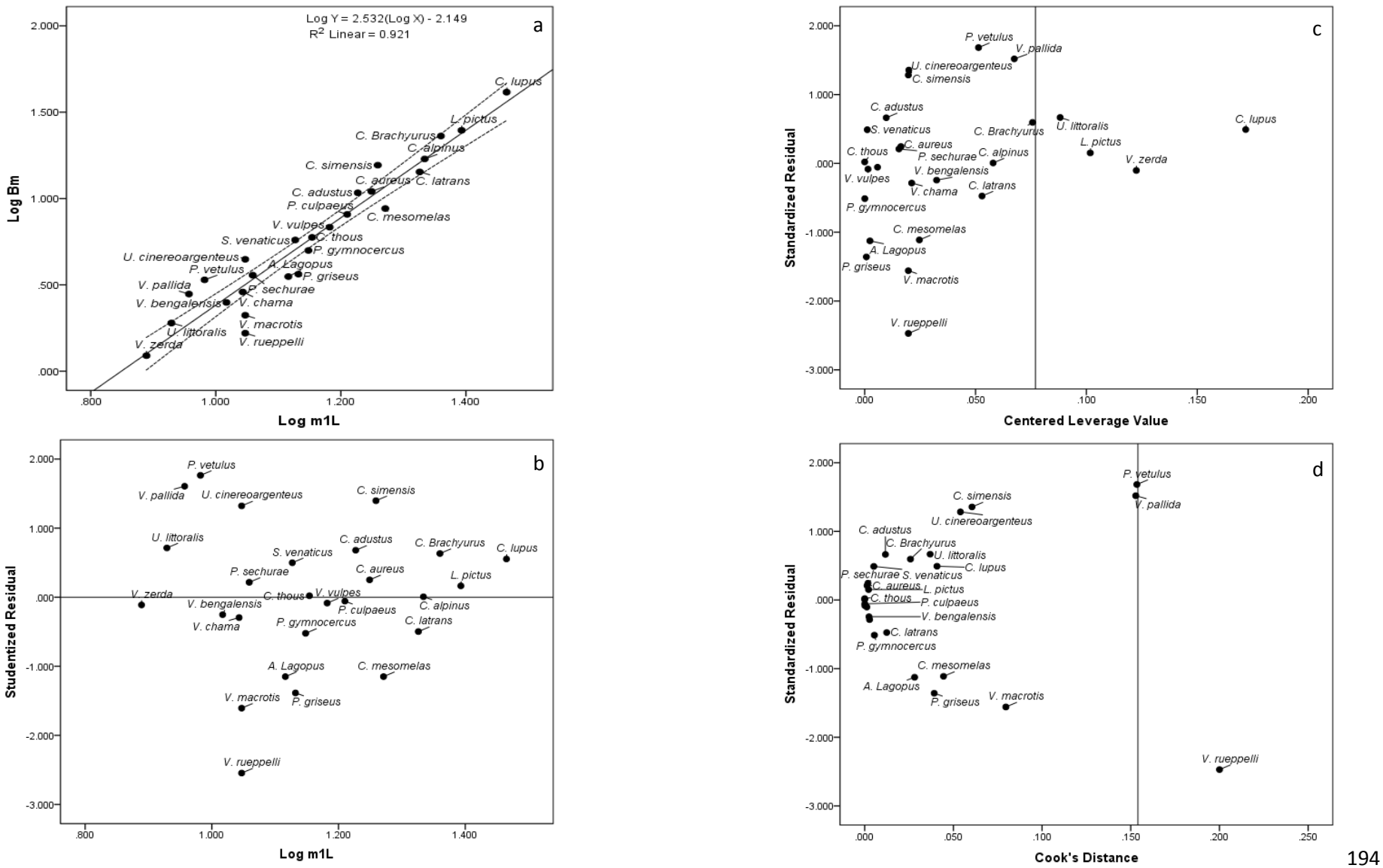


Figure 5.67. Least squares regression of body mass on m1L (regression 2). a). Regression line, b). Studentised residuals plotted with $\log_{10}$ m1L, c). Standardised residuals plotted with leverage, line indicating high leverage >0.077, d). Standardised residuals plotted with Cook's D, line indicating high influence >0.154.

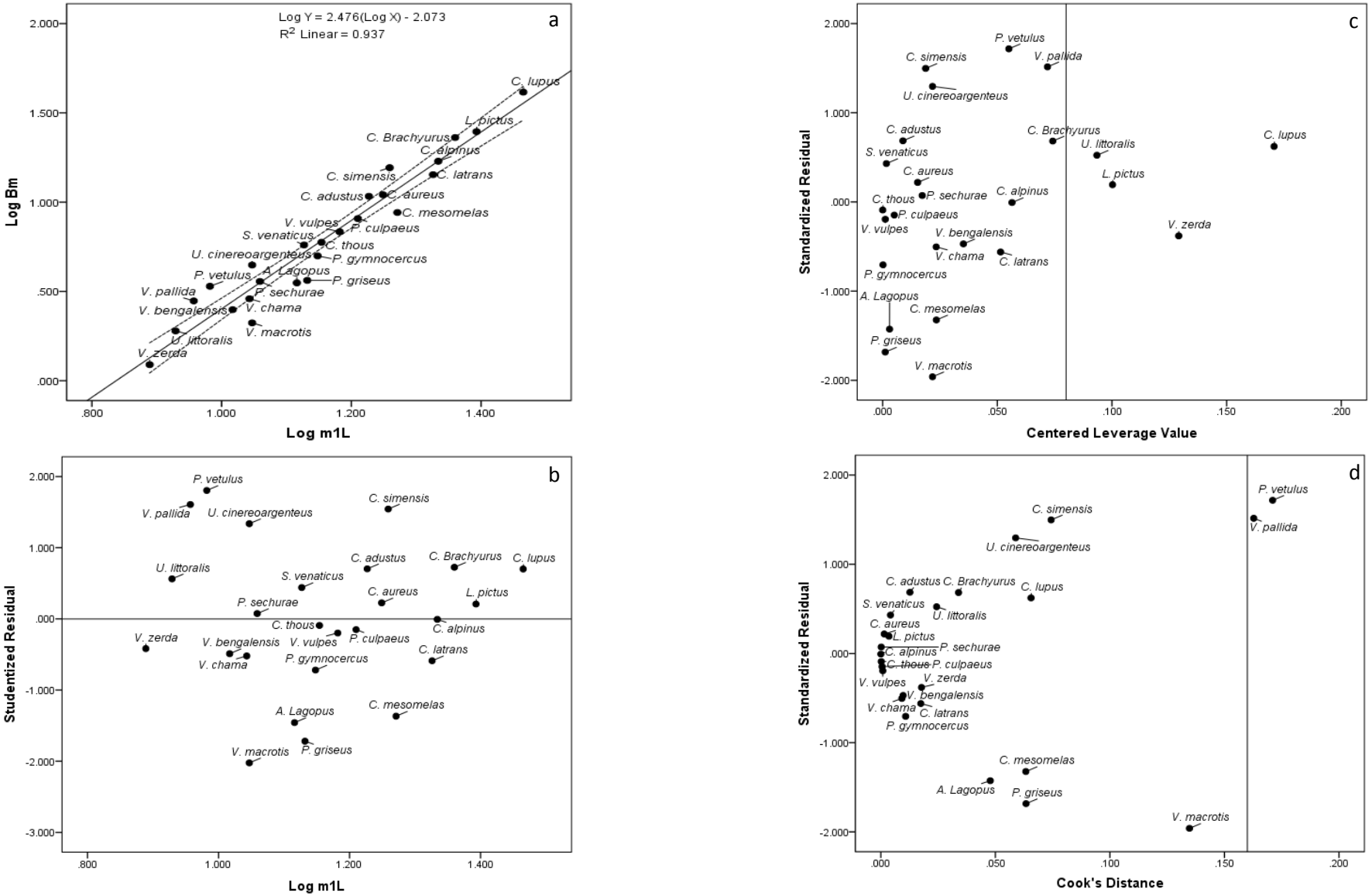


Figure 5.68. Least squares regression of body mass on m1L (regression 3). a). Regression line, b). Studentised residuals plotted with $\log_{10}$ m1L, c). Standardised residuals plotted with leverage, line indicating high leverage >0.080, d). Standardised residuals plotted with Cook's D, line indicating high influence >0.160.

Figure 5.68a indicates a strong positively linear correlation between body mass and m1L, with a significant Pearson correlation (r_{25} = 0.968, *p*=0.0001). Inspection of the residuals revealed no outliers (Figure 5.68b). However, *V. macrotis* had a studentised residual value of -2.024, just beyond the cut-off value of >2.0. As *V. macrotis* is slightly above this outlier cut-off value, leverage and influence were examined.

High leverage was indicated by values >0.080 (Figure 5.68c). *C. lupus, V. zerda. L. pictus* and *U. littoralis* were identified as having high leverage. However, these species all plot close to the regression line and are not outliers. High influence was indicated by values >0.160 (Figure 5.68d). *P. vetulus* and *V. pallida* were identified as having high influence but were equally not outliers. Further analysis of the residuals using Q-Q plots and Shapiro-Wilk test for normality indicated no outliers, and were found to be not non-normally distributed (Shapiro Wilk test W_{25} = 0.973, *p*=0.714).

Regression model 3 was therefore chosen to estimate body mass for the Pleistocene canids. Comparisons of the m1L regression line with that of P4L are shown in section 5.2.2.4.

5.2.2.2. Least squares regression of body mass on P4L

5.2.2.2.1. Regression 1

Least Squares regression of log_{10} transformed body mass on P4L was also performed using the 28 canid species dataset, despite the identification of outliers in Section 5.2.1.3 (Table 5.21 and Figure 5.69).

Regression number	Measure	n species	y-intercept (a)	slope (b)	r^2	SEE	t	*p*
1	P4L	28	-1.406	2.004	0.777	0.185	9.511	0.0001
2	P4L	27	-1.811	2.355	0.887	0.134	13.981	0.0001
3	**P4L**	**26**	**-1.743**	**2.304**	**0.903**	**0.122**	**14.927**	**0.0001**

Table 5.21 Results of least squares regression of body mass on P4L. Final regression model in bold.

Regression 1 was found as significant by ANOVA ($F_{1, 27}$ = 90.454, *p*=0.0001), highlighting the significant relationship between body mass and P4L. A *t*-test found the slope (*b*) highly significant (t=9.511, *p*=0.0001), also indicating the significance of the regression line. The high r^2 indicates moderately high correlation between body mass and P4L, as does the low SEE (Table 5.21).

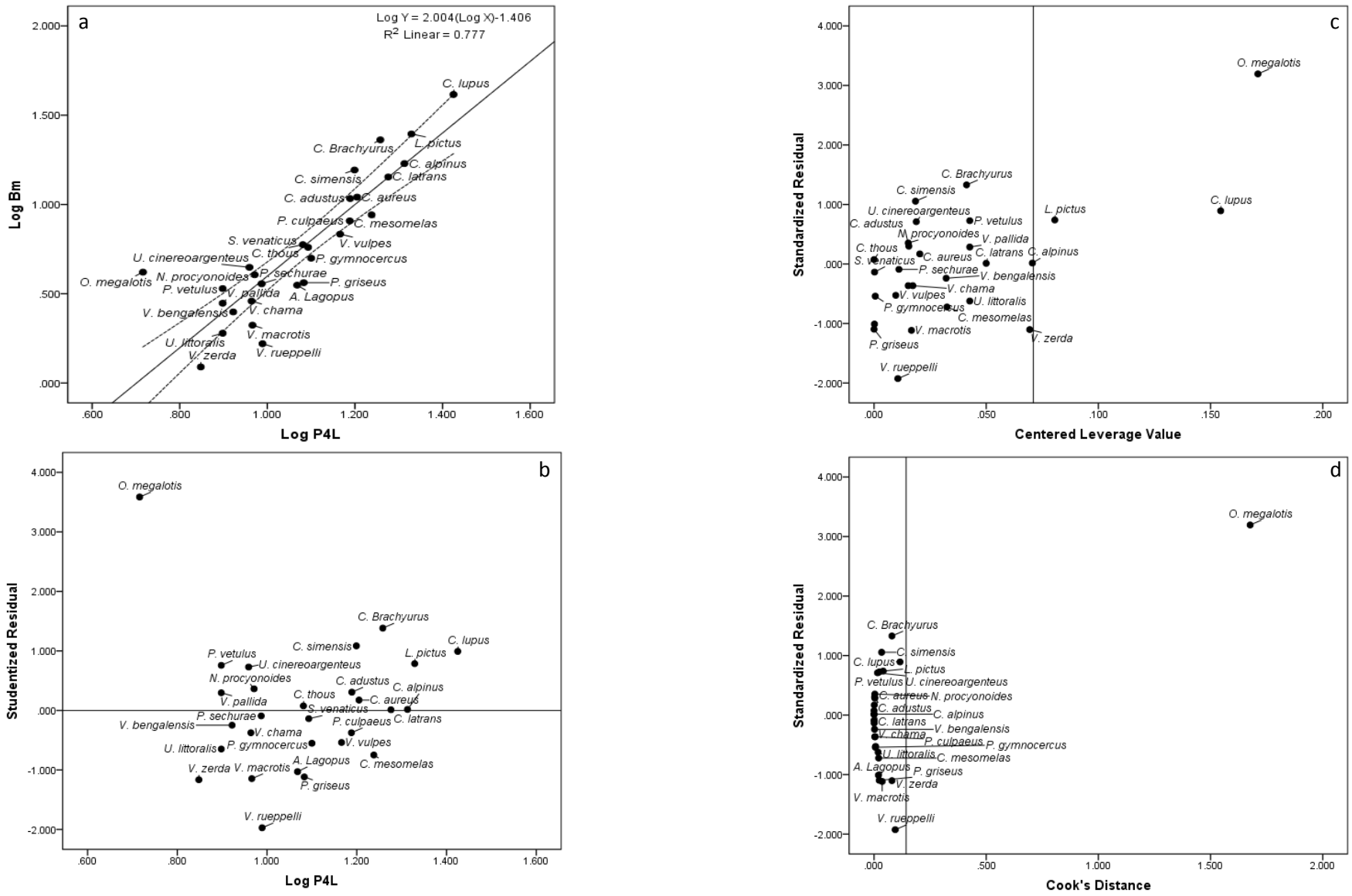


Figure 5.69. Least squares regression of body mass on P4L (regression 1). a). Regression line, b). Studentised residuals plotted with $\log_{10}$ P4L, c). Standardised residuals plotted with leverage, line indicating high leverage >0.071, d). Standardised residuals plotted with Cook's D, line indicating high influence >0.143.

Figure 5.69a reveals a strong positively linear correlation between body mass and P4L, found to be significant by Pearson correlation (r_{28} = 0.881, *p*=0.0001). *O. megalotis* was identified as an outlier and has a high residual value of 3.586 (Figure 6.69b), exceeding the >2 indicative of an outlier.

Leverage and influence were therefore assessed. *O. megalotis, C. lupus* and *L. pictus* were identified as having high leverage (values >0.071, Figure 5.69c), with *C. alpinus* on the cut-off point. However, only *O. megalotis* plots away from the bulk of the data explained by the regression line and was also shown to have high influence (values >0.143) (Figure 5.69d).

The residuals were also checked for outliers and normality using Q-Q plot and Shapiro-Wilk test. As expected *O. megalotis* was identified as an outlier, with the residuals found to be not non-normally distributed (Shapiro-Wilk test W_{28} = 0.935, *p*=0.081). As *O. megalotis* was identified as an outlier with high influence, albeit low leverage, this species was removed from the regression model.

5.2.2.2.2. Regression 2

Following the removal of *O. megalotis*, body mass was regressed on P4L using the revised 27 species dataset (Table 5.21 and Figure 5.70).

Regression 2 was found as significant by ANOVA ($F_{1, 26}$ = 195.466, *p*=0.0001), highlighting the significant relationship between body mass and P4L. A *t*-test found the slope (*b*) highly significant (t=13.981, *p*=0.0001), indicating the significance of the regression line. With the removal of *O. megalotis*, the r^2 has increased, and the SEE has decreased (Table 5.21).

Figure 5.70a indicates a strong positively linear correlation between body mass and P4L, found as significant by Pearson correlation (r_{27} = 0.942, *p*=0.0001). *V. rueppelli* is also indicated as plotting further from the main body of the data. Further inspection of the residuals reveals *V. rueppelli* as an outlier with a high studentised residual of -2.221 (Figure 5.70b).

Leverage and influence were therefore assessed, with high leverage indicated by values >0.074 found for *C. lupus, V. zerda, L. pictus* and *C. alpinus*, none of which were outliers. High influence was indicated by values >0.148 and was identified in *P. vetulus* and *V. rueppelli*, with *V. rueppelli* just above the cut-off with a value of 0.149.

Again, residuals were also checked for outliers and normality using Q-Q plot and a Shapiro-Wilk test. *V. rueppelli* was again identified as an outlier, although the residuals were found to be not non-normally distributed (Shapiro-Wilk test W_{27} = 0.978, *p*=0.824). Even though *V. rueppelli* had low leverage and only slightly high influence, it was removed from the regression model due to being an outlier in the residuals.

5.2.2.2.3. Regression 3

With the removal of *O. megalotis* and *V. rueppelli*, body mass was regressed on P4L using the revised 26 species dataset (5.21 and Figure 5.71).

Regression 3 was found to be significant by ANOVA ($F_{1, 24}$ = 222.820, *p*=0.0001), highlighting the significant relationship between body mass and P4L. A *t*-test found the slope (*b*) highly significant (t=14.927, *p*=0.0001), indicating the significance of the regression line. From the removal of outlier species, the r^2 of the model has increased, and the SEE decreased further (Table 5.21).

Figure 5.71a illustrates a strong positively linear correlation between body mass and P4L, with a significant Pearson correlation (r_{26} = 0.950, *p*=0.0001). Further inspection of the residuals indicated no further outliers were present, with all residual values >2.0. Although no outliers were identified in the residuals, leverage and influence were still assessed.

C. lupus, V. zerda and *L. pictus* were identified as having high leverage (values >0.077). However these species all plot close to the regression line with the bulk of the data are not apparent outliers. High influence was indicated by values >0.154. *P. vetulus* was identified as having high influence, although not defined as a residual outlier.

The residuals were also checked for outliers and normality using Q-Q plot and Shapiro-Wilk test. No outliers were identified, and the residuals were found to be not non-normally distributed (Shapiro-Wilk test W_{26} = 0.959, *p*=0.371).

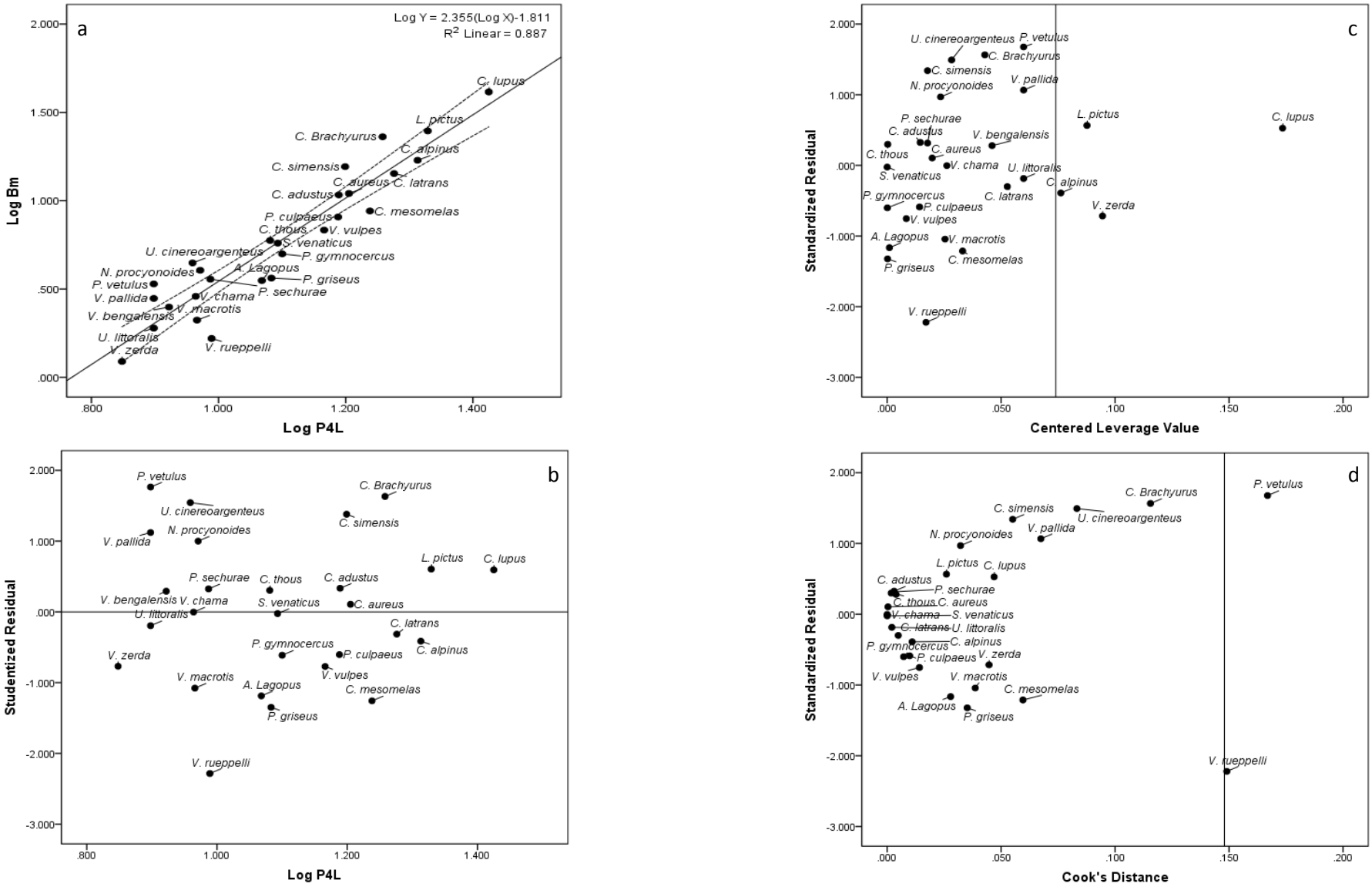


Figure 5.70. Least squares regression of body mass on P4L (regression 2). a). Regression line, b). Studentised residuals plotted with $\log_{10}$ P4L, c). Standardised residuals plotted with leverage, line indicating high leverage >0.074, d). Standardised residuals plotted with Cook's D, line indicating high influence >0.148.

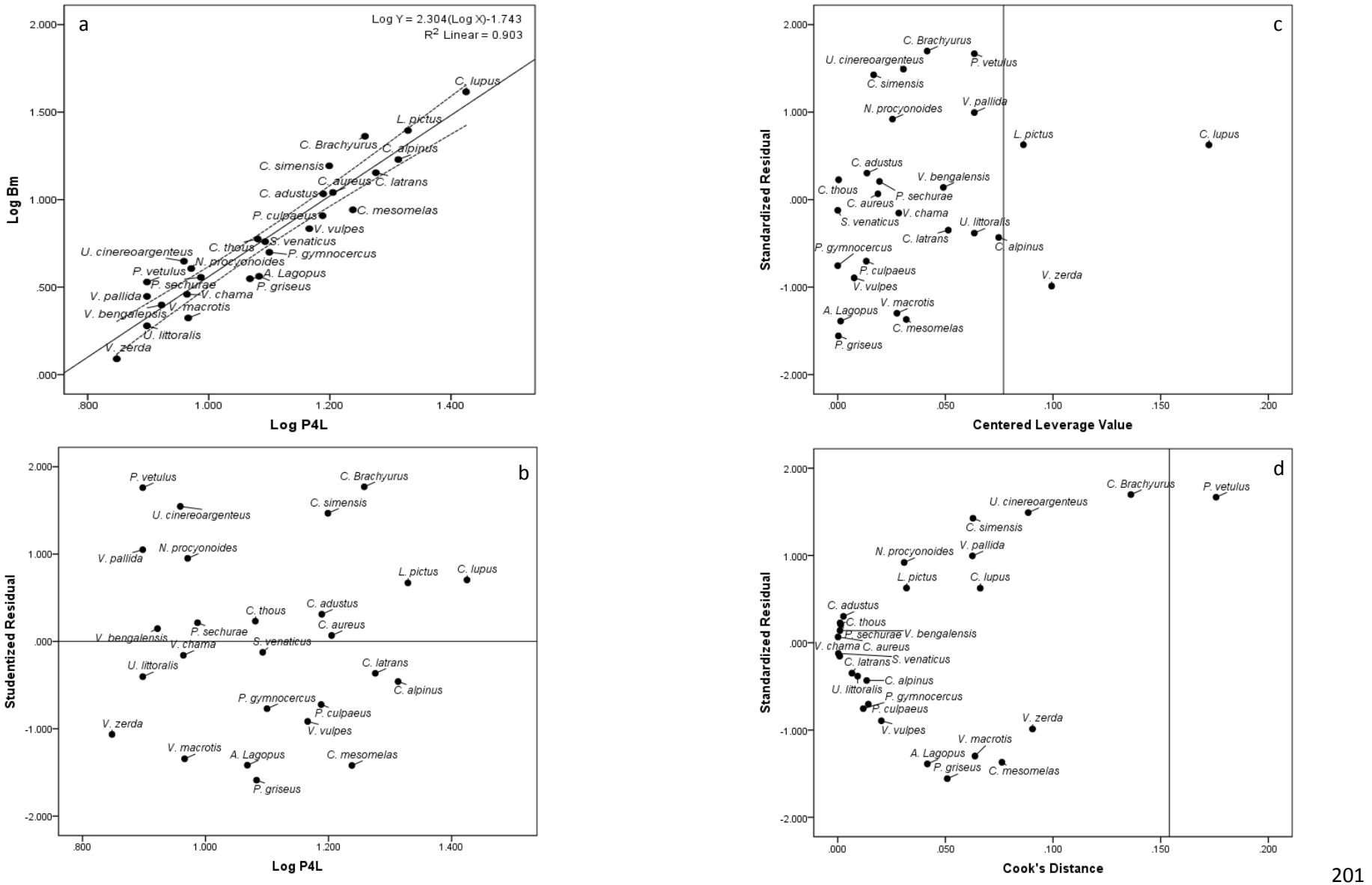


Figure 5.71. Least squares regression of body mass on P4L (regression 3). a). Regression line, b). Studentised residuals plotted with $\log_{10}$ P4L, c). Standardised residuals plotted with leverage, line indicating high leverage >0.077, d). Standardised residuals plotted with Cook's D, line indicating high influence >0.154.

As no outliers were identified, and species with high leverage and high influence were not outliers in their residuals, body mass of the Pleistocene canids was estimated using the third regression model for P4L. Comparison of the chosen regression for m1L and P4L is shown in the following section.

5.2.2.4. Comparing the regression equations for m1L and P4L

To test whether the slopes of the chosen two regressions for m1L and P4L are significantly different from each other, a Student's *t* test was used based on the following equation from Zar (2010):

$$t = \frac{b_1 - b_2}{Sb_1 - b_2}$$

Where *t* = *t* test statistic, *b* = slope, S*b* = standard error of slope, with α = 0.05, d.f. = n-2.

The slopes were tested using the H_0: $\beta_1 = \beta_2$, that the slope from the regression of body mass and m1L equals the slope of body mass and P4L. The H_0 is rejected if the calculated t is greater than the critical value of t, shown as $t \geq t_{0.05\,(2),\,47}$.

Hence, for m1L, Slope $b_1 = 2.476$, with $Sb_1 = 0.133$, d.f. = 23, and for P4L, Slope $b_2 = 2.304$, d.f. = 24. This calculates a *t* = 0.07923. This value is less than the critical value of t ($t_{0.05\,(2),\,47}$ = 2.0117), and therefore the H_0 is retained, with no significant differences apparent between the slopes.

Based on the equation (log body mass = b (log measure)+ a Where b: slope, a: y-intercept), the results of the body mass regressions for m1L and P4L (Table 5.22) can be expressed as:

Log Y = 2.476(logm1L) - 2.073 *and* Log Y = 2.304(logP4L) - 1.743

Measure	**n**	**y-intercept (a)**	**slope (b)**	**slope (b) CI 95%**	**r^2**	**SEE**	**%SEE**	**%PE**	**QMLE**	**RE**
m1L	25	-2.073	2.476	2.200 - 2.752	0.937	0.100	25.75	17.49, (17.41 QMLE)	1.006	1.038
P4L	26	-1.743	2.304	1.985- 2.622	0.903	0.122	32.41	23.82, (23.59 QMLE)	1.009	1.069

Table 5.22. Results from least squares regression of m1L and P4L. Correction factors (QMLE, RE) shown. *t* values and *p* values (2 tailed d.f=n-2) for slopes shown in Table 5.20 (for m1L) and Table 5.21 (for P4L).

The r^2 is given, and the %SEE and %PE calculated to determine the prediction error of both regression models. The r^2 for both regressions is high, with the best result from m1L (r^2 = 0.937).

As introduced in Chapter 4, the %SEE provides a measure of predictive precision, with low %SEE indicating the regression equation to be more accurate at predicting body mass (Van Valkenburgh, 1990). When comparing the %SEE for both regressions, m1L is the more accurate, with the lower %SEE.

A low %PE also is an indication of the accuracy of the regression equation at predicting body mass. When compared, m1L also has the lower %PE, however, the %PE is still indicating a 17.41% error in the prediction of body masses. Based on the higher r^2, and lower %SEE and %PE, m1L was chosen to estimate Pleistocene canid body masses.

5.2.3. Estimating Pleistocene canid body mass

As outlined in Chapter 4, bias is caused by the de-transformation of logarithms back into arithmetic units and correction factors must be applied.

Based on correction factor values shown in Table 5.22, for m1L, QMLE indicated 0.6% bias present, whereas RE indicated 3.8% bias, with a difference of 3% existing between the two correction factors. For P4L, QMLE indicates 0.9% bias, and RE indicates 6.9% bias, with a difference of 6% between the two correction factors.

For m1L, since only 3% difference is present between the correction factors, and because of the relative ease of applying QMLE to published data (that have not applied a correction factor), QMLE was used in the estimation of the Pleistocene canid body mass and applied to all de-transformed body mass values.

Table 5.23 shows the estimated body masses of the Pleistocene canids using m1L (see previous section for equation). Body masses estimated using P4L shown for comparison. 95% confidence intervals were calculated for each estimate.

Species	Predictor	n	Estimated mean body mass (Kg)*	95% CI (Kg)	BM range based on 95% CI (Kg)
Pleistocene *C. lupus*	m1L	75	35.81	± 1.59	34.22-37.40
	P4L	24	34.07	± 1.81	32.26-35.88
C. mosbachensis	m1L	25	22.50	± 1.62	20.85-24.19
	P4L	13	23.84	± 1.87	21.97-25.71
C. arnensis	m1L	9	17.94	± 1.73	16.21-19.67
	P4L	3	18.49	± 35.63	-17.41-54.12

C. etruscus	m1L	15	24.34	± 1.65	22.69-25.99
	P4L	7	23.73	± 2.08	21.65-25.81

Table 5.23. Estimated mean Pleistocene canid body mass using m1L. For comparison, estimates using P4L included. *QMLE correction factor used for bias. 95% CI and range shown.

Table 5.23 reveals that body mass estimates derived from m1L and P4L are similar for each species. Out of the Pleistocene canids studied, Pleistocene *C. lupus* was the largest with a body mass estimate of 35.81Kg (± 1.59 Kg) (Figure 5.72), indicating that Pleistocene wolves were lighter than their modern counterparts. However, modern *C. lupus* exhibits a large range in body mass, from 18-80Kg including both sexes (Mech, 1974). As this is a range and not a confidence interval, it is not shown on Fig. 5.72. Here, mean body mass is calculated from a range of sources (see Table 5.17) as 41.33Kg. The reconstructed Pleistocene body mass therefore falls within the range of modern *C. lupus* body mass.

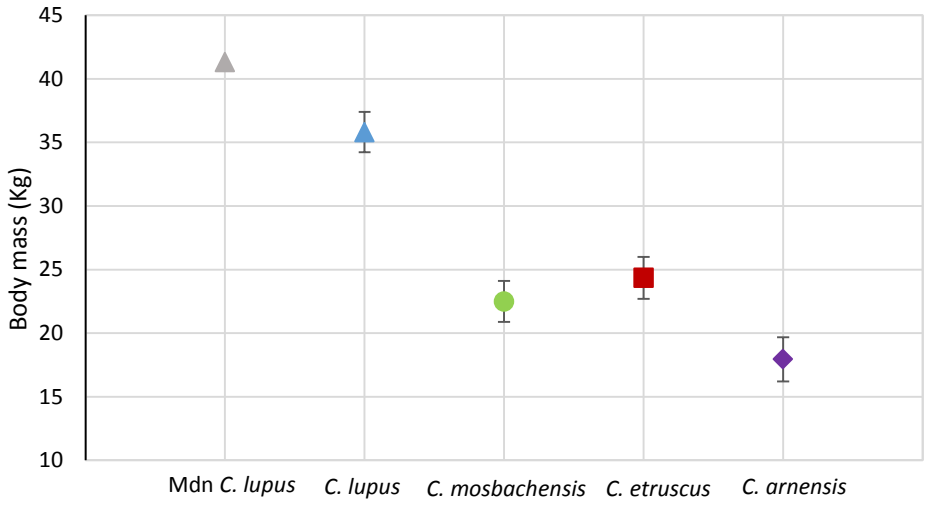


Figure 5.72. Plot illustrating estimated mean body masses of Pleistocene *C. lupus, C. mosbachensis, C. etruscus and C. arnensis*. Modern (Mdn) *C. lupus* mean body weight included for comparison. Error bars represent 95% CI (Table 5.23).

The body masses of the other Pleistocene canids were lighter than modern and Pleistocene *C. lupus* (Fig. 5.72). C*. mosbachensis*, with an estimate of 22.50 ± 1.62Kg, was found to be slightly lighter than *C. etruscus* (estimated at 24.34 ± 1.65Kg), although within its 95% CI, and *C. arnensis* much lighter still, at 17.94 ± 1.73Kg.

5.2.3.1. Body mass estimation for Pleistocene *C. lupus*

Using the body mass estimating equation Log Y = 2.476(logm1L) - 2.073, body masses were estimated for Pleistocene *C. lupus* from Britain and mainland Europe by age group and by site (Tables 5.24 and 5.25).

C. lupus	MIS	n	estimated mean body mass (Kg)	95% CI (Kg)	BM range based on 95% CI
All Pleistocene Britain	all	59	36.25	± 1.59	34.66-37.84
By age group	2	2	38.57	N/A	
	3	20	35.40	± 1.63	33.77-37.03
	5a	18	39.85	± 1.64	38.21-41.49
	5c	2	35.20	N/A	
	5e	4	33.54	± 2.70	30.84-36.24
	6	4	32.18	± 2.70	29.48-34.88
	7	9	34.03	± 1.73	32.30-35.76

Table 5.24. Estimated mean body masses (Kg) from m1L of Pleistocene *C. lupus* from Britain by age groups. Mean body mass and 95% CI calculated for age groups with >2 individuals.

For age groups containing less than three individuals, confidence intervals could not be calculated due a lack in degrees of freedom (Figure 5.73).

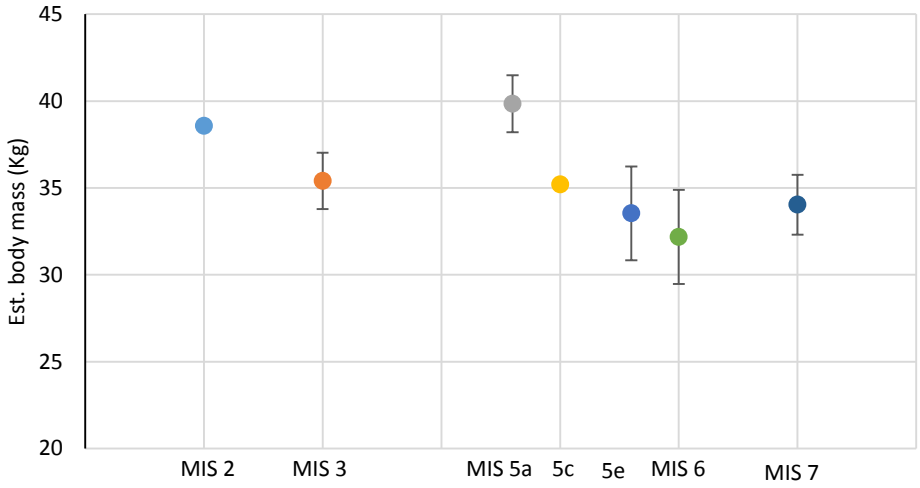


Figure 5.73. Plot illustrating estimated mean body masses for Pleistocene *C. lupus* from Britain. 95% CI shown where applicable.

The combined sample of Pleistocene *C. lupus* from Britain has an estimated body mass of 36.25Kg ± 1.59Kg. However, variations are apparent when examining the dataset at finer chronological resolution. The MIS 5a group has the largest mean body mass, with its range encompassing recent *C. lupus* mean body mass (41.33Kg), whereas specimens from MIS 3, 5e, 6 and 7 overlap in their mass ranges.

Table 5.25 shows the body mass estimates for Pleistocene *C. lupus* by site in Britain.

Site	MIS	n	Estimated mean body mass (Kg)	95% CI (Kg)	BM range based on 95% CI
Cae Gwyn Cave	2	1	N/A	N/A	
Ogof yr Ychen	2	1	N/A	N/A	
Black Rock Quarry	3	3	37.14	± 18.5	18.64-55.64

Kents Cavern (Cave Earth)	3	4	34.69	± 2.70	31.99-37.39
Oreston Cave	3	5	33.38	± 2.09	31.29-35.47
Paviland	3	5	37.44	± 2.09	35.35-39.53
Pin Hole Cave	3	2	32.42	N/A	
Sandford Hill	3	1	N/A	N/A	
Banwell Bone Cave	5a	13	39.24	± 0.65	38.59-39.89
Bosco's Den	5a	1	N/A		
Windy Knoll	5a	1	N/A		
Wretton	5a	1	N/A		
Steetley Quarry Cave	5a	1	N/A		
Stump Cross Cave	5a	1	N/A		
Bacon Hole	5c	1	N/A		
Minchin Hole	5c	1	N/A		
Barrington	5e	1	N/A		
Joint Mitnor Cave	5e	3	33.69	± 18.5	15.19-52.19
Clevedon Cave	6	4	32.18	± 2.70	29.48-34.88
Bleadon Cave	7	2	38.12	N/A	
Crayford	7	1	N/A	N/A	
Hutton Cave	7	2	33.16	N/A	
Ilford	7	1	N/A	N/A	
Marsworth	7	2	32.37	N/A	
Tornewton Cave (Otter stratum)	7	1	N/A	N/A	

Table 5.25. Estimated mean body mass (Kg) of *C. lupus* by site in Britain. Mean and CI calculated for sites with >2 individuals.

It was not possible to estimate body mass for many of the sites due to low numbers of individuals. Body mass varies between sites of the same age (e.g. MIS 3), although estimates overlap in their confidence interval ranges. Banwell Bone Cave had the largest estimated mean body mass, whilst Clevedon Cave had the smallest.

Table 5.26 shows the estimated body masses for Pleistocene *C. lupus* from mainland Europe.

C. lupus	**Age group**	**n**	**Estimated mean body mass (Kg)**	**95% CI (Kg)**	**BM range based on 95% CI (Kg)**
All Pleistocene Europe	all	16	34.23	± 1.64	32.59-35.87
By age group	2.4	4	36.00	± 2.70	33.30-38.70
	2.8	8	34.51	± 1.76	32.75-36.27
	3	3	30.65	± 18.5	12.15-49.15

Table 5.26 Estimated mean body masses (Kg) of Pleistocene *C. lupus* from European mainland by age groups. Mean body mass and 95% CI calculated for age groups with >2 individuals.

Estimated mean body mass for Pleistocene *C. lupus* from mainland Europe (Table 5.27) appears lighter than from Britain, although within the 95% confidence interval. This may relate to the comparatively low number of individuals recorded.

Site	Age group	n	Estimated mean body mass (Kg)	95% CI (Kg)	BM range based on 95% CI (Kg)
Grotta di Paglicci	2	1	N/A		
Perick Cave	2.4	3	36.66	± 18.50	18.16-55.16
Ranis	2.4	1	N/A		
Bad Canstatt, Villa Seckendorf	2.8	6	34.85	± 1.90	32.95-36.75
Taubach	2.8	1	N/A		
Monte Tignoso	2.8	1	N/A		
Dobelhaldeschacht	3	1	N/A		
Weimar-Ehringsdorf	3	2	31.46	N/A	

Table 5.27. Estimated mean body mass (Kg) of Pleistocene *C. lupus* by site in Europe. Mean and CI calculated for sites with >2 individuals.

Due to low numbers of individuals, estimates were only possible from Perick Cave and Bad Canstatt (Villa Seckendorf), although the low number of individuals inflates the 95% confidence limit for Perick Cave.

5.2.3.2. Body mass estimates *C. mosbachensis*

Using the same body mass estimating equation Log Y = 2.476(logm1L) - 2.073, body masses were estimated for *C. mosbachensis* from Britain and mainland Europe by age group and by site (Table 5.28). The estimated body mass for *C. mosbachensis* from Britain is 22.47 ± 1.69Kg. MIS 13 was the only age group containing enough individuals for body mass to be estimated.

C. mosbachensis	MIS	n	Estimated mean body mass	95% CI (Kg)	BM range based on 95% CI (Kg)
All Pleistocene Britain	all	11	22.47	± 1.69	20.78-24.16
Age group	13	10	22.07	± 1.71	20.36-23.78

Table 5.28. Estimated mean body masses (Kg) of *C. mosbachensis* from Britain by age groups. Mean body mass and 95% CI calculated for age groups with >2 individuals.

Table 5.29 shows the estimated body masses of *C. mosbachensis* by site.

Site	MIS	n	Estimated mean body mass	95% CI (Kg)	BM range based on 95% CI (Kg)
Boxgrove	13	3	20.34	± 18.50	1.85-38.84
Sidestrand	13	1	N/A		
Westbury-sub Mendip	13	6	22.35	± 1.90	20.45-24.25

Table 5.29. Estimated mean body mass (Kg) of *C. mosbachensis* by site in Britain. Mean and 95% CI calculated for sites with >2 individuals.

The low number of individuals at Boxgrove caused wide confidence limits for the estimated body mass (20.34 ± 18.50Kg). The estimates for Westbury-sub-Mendip, however, have narrower confidence limits (22.35 ± 1.90Kg).

Table 5.30 shows the body mass estimates for *C. mosbachensis* from mainland Europe.

C. mosbachensis	**Age group**	**n**	**Estimated mean body mass**	**95% CI (Kg)**	**BM range based on 95% CI (Kg)**
All Pleistocene Europe	3.4-4	13	22.52	± 1.67	20.85-24.19
Age group	3.4	3	20.52	± 18.50	2.02-39.02
	4	10	23.14	± 1.71	21.43-24.85

Table 5.30 Estimated mean body masses (Kg) of *C. mosbachensis* from mainland Europe by age groups. Mean body mass and 95% CI calculated for age groups with >2 individuals.

The body mass estimates for mainland Europe were similar to those from Britain for *C. mosbachensis*, with further similarity noted between Early Pleistocene continental *C. mosbachensis* and the MIS 13 *C. mosbachensis*.

Table 5.31 shows the estimated body masses for *C. mosbachensis* from mainland Europe by site. Body mass estimates were only possible for Untermassfeld, due to low numbers of individuals at other European sites.

Site	**Age group**	**n**	**Estimated mean body mass**	**95% CI (Kg)**	**BM range based on 95% CI (Kg)**
Heppenloch	3.4	1	N/A		
Monte Zoppega	3.4	2	18.36	N/A	
Untermassfeld	4	10	23.14	± 1.71	21.43-24.85

Table 5.31. Estimated mean body mass (Kg) of Pleistocene *C. mosbachensis* by site in mainland Europe. Mean and 95% CI calculated for sites with >2 individuals.

5.2.3.3. Body mass estimates *C. arnensis* and *C. etruscus*

Using the same body mass estimating equation Log Y = 2.476(logm1L) - 2.073, body masses were reconstructed for *C. arnensis* and *C. etruscus* from mainland Europe by age group and by site (Table 5.32).

Species	**Age group**	**n**	**Estimated mean body mass**	**95% CI (Kg)**	**BM range based on 95% CI (Kg)**
C. arnensis	4.4	9	17.94	± 1.73	16.21-19.67
C. etruscus	4.4	15	24.34	± 1.65	22.69-25.99
Upper Valdarno	4.4	11	23.91	± 1.69	22.22-25.60
Val di Magra (Olivola)	4.4	4	25.55	± 2.70	22.85-28.25

Table 5.32 Estimated mean body masses (Kg) of *C. arnensis* and *C. etruscus* from mainland Europe by age groups. Mean body mass and 95% CI calculated for age groups with >2 individuals.

Since *C. arnensis* material was only available from the Upper Valdarno Basin, the estimate for the locality also serves as the body mass estimate for the species. For *C. etruscus*, however, material was recorded from both the Upper Valdarno basin and Val di Magra (Olivola). As indicated in Table 5.32, *C. etruscus* is heavier than *C. arnensis* (24.34 ± 1.65Kg and 17.94 ± 1.73Kg respectively). Estimated body mass for *C. etruscus* at Val di Magra (Olivola) and Upper Valdarno basin are similar and lie within range of one other.

5.2.4. Comparison with estimates from Van Valkenburgh's (1990) predictive equation

The body mass estimates for the Pleistocene canids generated above were then compared to another predictive equation based on a sample of 14 extant canids (Van Valkenburgh, 1990) in order to examine which equation provided greater refinement and more accuracy. When compared, the predictive equation produced by this research (Log Y = 2.476(logm1L) - 2.073) has %SEE of 25.75 and %PE of 17.41 (see Table 5.22 for full results). In comparison to Van Valkenburgh (1990) (Log Y = 1.82(Logm1L)-1.22, r = 0.87, SE = 0.158, %SEE = 44, %PE = 27), it has a lower %SEE and %PE, indicating a more accurate estimation of body mass. Table 5.33 compares the body masses of the Pleistocene canids calculated from both predictive equations.

Species	**Estimated mean body mass (Kg)* 95% CI (Kg)**	**Estimated mean body mass (Kg) Van Valkenburgh (1990)****
Pleistocene *C. lupus*	35.81 ± 1.59	28.20 ±2.09
C. mosbachensis	22.50 ± 1.62	20.03 ±2.16
C. arnensis	17.94 ± 1.73	16.90 ±2.40
C. etruscus	24.34 ± 1.65	21.23 ±4.85

Table 5.33. Comparison of predictive equations using m1L. Estimated body mass for Pleistocene canids calculated from both equations. 95% CI shown. *QMLE applied to de-transformed mean body mass estimates.**QMLE was calculated here for Van Valkenburgh's (1990) equation in lieu of its absence.

In comparison, the equation created by this present research is more accurate than Van Valkenburgh (1990) predictive equation, with lower %SEE and %PE. Nonetheless, it is interesting to compare the different estimates of body mass calculated by each equation. The predictive equation created in this study estimates higher body masses, with narrower

confidence intervals, with the lower %SEE and %PE representing higher predictive power and precision.

5.2.5. Sexual dimorphism in modern *C. lupus*

Evidence for sexual dimorphism in modern European *C. lupus* was investigated following Dayan et al. (1992). Using a smaller group of measurements (p4L, m1L, m1W, m2L, p1m3L, m1m2D, P4L, P4W, M1L, M1W, M1M2L and condylobasal skull length [SKL] only), the mean, standard deviation and coefficient of variation (CV) of the male and female measurements were established, and the percentage of sexual dimorphism was calculated as the difference between the mean male and female measurements (Table 5.34). Significant differences between males and females were investigated using independent sample *t*-tests, with variances examined using Levene's tests (also Table 5.34).

Measure	Sex	n	Mean	SD	CV	% sd	Levene's test	*t* test
p4L	M	31	15.89	0.668	4.204	5.11%	F_{51} = 0.384, p=0.538	t_{51} = 4.698, p=0.0001
	F	22	15.08	0.543	3.603			
m1L	M	31	30.17	1.241	4.115	6.94%	F_{51} = 0.018, p=0.894	t_{51} = 5.830, p=0.0001
	F	22	28.08	1.352	4.815			
m1W	M	31	12.10	0.529	4.374	8.02%	F_{51} = 0.187, p=0.667	t_{51} = 6.637, p=0.0001
	F	22	11.13	0.517	4.648			
m2L	M	30	12.16	0.695	5.721	2.27%	F_{49} = 0.821, p=0.369	t_{49} = 1.465, p=0.149
	F	21	11.88	0.610	5.138			
p1m3L	M	30	97.35	3.248	3.337	3.98%	F_{49} = 1.201, p=0.279	t_{49} = 4.715, p=0.0001
	F	21	93.47	2.265	2.423			
m1m2D	M	31	33.73	3.062	9.079	6.36%	F_{51} = 0.013, p=0.909	t_{51} = 2.435, p=0.018
	F	22	31.59	3.300	10.449			
P4L	M	30	27.24	1.060	3.891	6.86%	F_{50} = 1.796, p=0.186	t_{50} = 6.820, p=0.0001
	F	22	25.37	0.847	3.340			
P4W	M	30	14.68	0.928	6.324	7.14%	F_{50} = 0.547, p=0.463	t_{50} = 4.214, p=0.0001
	F	22	13.63	0.825	6.056			
M1L	M	31	17.32	0.909	5.249	4.5%	F_{52} = 0.125, p=0.725	t_{52} = 3.209, p=0.002
	F	23	16.54	0.844	5.103			
M1W	M	31	23.36	1.445	6.186	6.14%	F_{52} = 0.040, p=0.842	t_{52} = 3.718, p=0.0001
	F	23	21.92	1.341	6.119			
M1M2L	M	31	23.92	1.627	6.490	4.62%	F_{52} = 0.044, p=0.834	t_{52} = 2.565, p=0.013
	F	23	22.82	1.481	6.802			
SKL	M	30	242.20	9.796	4.045	4.81%	F_{50} = 0.032, p=0.858	t_{50} = 4.343, p=0.0001
	F	22	230.55	9.226	4.002			

Table 5.34. Sexual dimorphism in modern European *C. lupus*. Sex, number (n), mean, standard deviation (SD) given for males and females. Coefficient of variation (CV) and percentage of sexual dimorphism (%sd) calculated. Males and females tested for equality of variances (Levene's test) and for significant differences (*t* tests), significance indicated by $p<0.05$.

The CV and %sd are illustrated in Figure 5.74. The percentage of sexual dimorphism ranges from 2.27-8.02% for modern *C. lupus*, with the lowest amount of dimorphism in m2L, and the highest in m1W. Variances were equal for all measurements from Levene's tests. *t* tests found all but m2L to be significant ($p<0.05$). m2L was the least sexually dimorphic measurement and showed no significant difference between males and females.

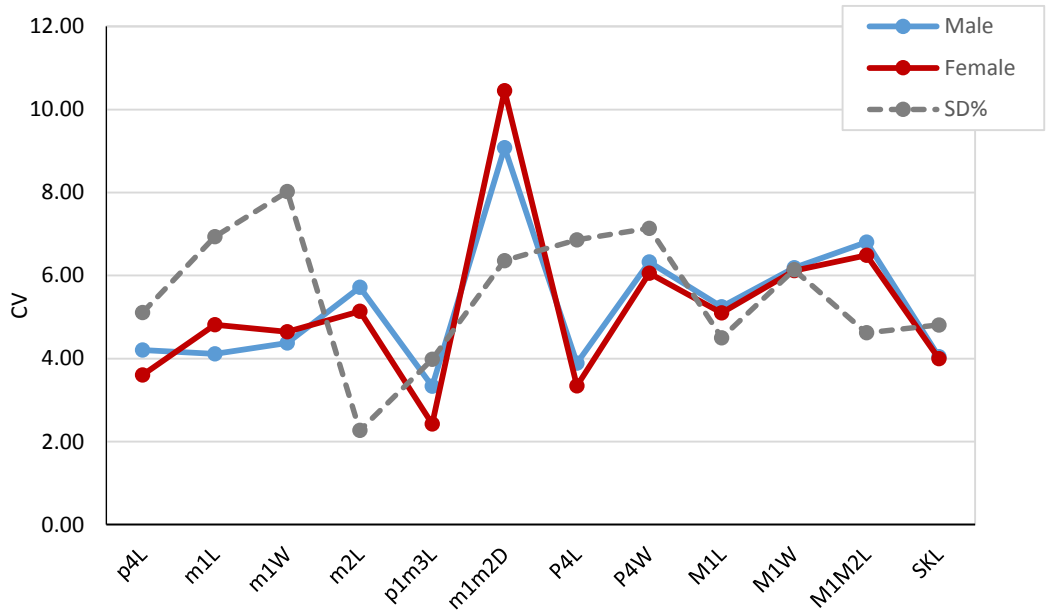


Figure 5.74. Plot showing C.V. of selected measurements for males and females of modern European *C. lupus* and percentage of sexual dimorphism (%sd).

The CV for males and females is relatively similar for each measurement. For the CV, m1m2D is the most variable measurement, with p1m3L, P4L and SKL the least variable between the sexes. Measurements of the lower carnassial are slightly more variable than those of the upper carnassial, although in contrast, m1L and W vary more symmetrically than P4L and W. The percentage of sexual dimorphism for each measure, however, is much more varied between measurements, with m1W having the highest percentage of dimorphism, and m2L the lowest.

5.2.6. Bergmann's Rule and modern European *C. lupus*

Using the modern European *C. lupus* dataset, a key aim was explore whether any changes in size could be observed to correlate with latitude (see Chapter 3). The modern wolf dataset contains individuals from Sweden, France, Spain, Portugal, Serbia, Bosnia, Poland and Russia (illustrated in Chapter 4, Figure 4.5). The wolves from Sweden and Russia represent the high latitude population (>55°N), with the remaining wolves grouped into the

lower latitude group for southern Europe (<55°N) (latitudes shown in Table 4.3.). As only actual body weight at death was available for some *C. lupus* from Sweden only, m1L was used as a proxy for body size, and was found to be significantly different between males and females (t_{51} = 5.830, p=0.0001). Figure 5.75a illustrates the latitude of individuals, with Figure 5.75b separating the individuals by sex.

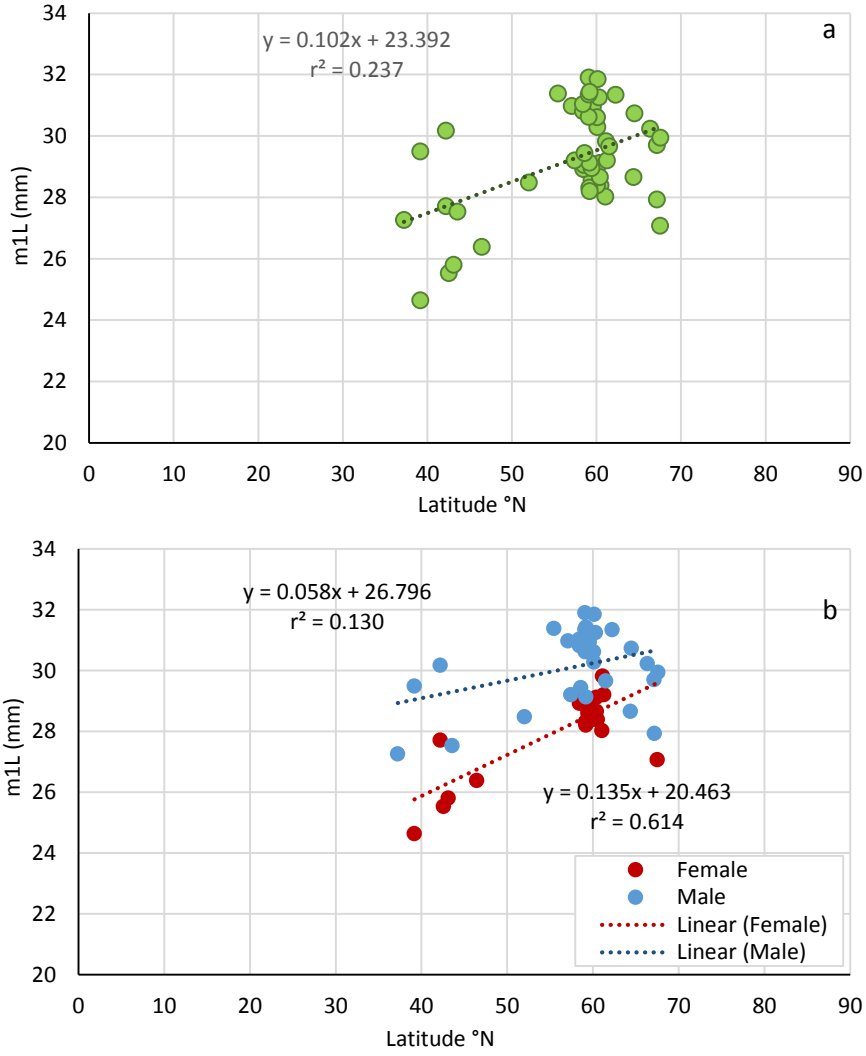


Figure 5.75. Plots showing m1L and latitude for modern European *C. lupus*. a) All individuals, with regression line for all data with equation and r^2 b). Individuals separated by sex, with regression lines for each sex shown with regression equation and r^2.

The modern European *C. lupus* data extend from mid Portugal at 39°N to the Arctic Circle in Sweden at 67°N. The r^2 shown in Figure 5.75a indicates that the relationship between latitude and m1L does not account for all the variation present in the data. As Figure 5.75a shows, the majority of data is from central Sweden, with fewer individuals from northern Sweden. This group contains the largest m1L of the European dataset, inferred to be the largest individuals.

The high latitude data can be separated into two groups, and as highlighted by Figure 5.75b, this grouping is based on sex, with males having larger m1L (and consequently larger body size) than females from the same latitude.

The lower latitude individuals represent more southern European wolves. This group contains the smallest m1L measurements, and hence proposed smaller body sizes. Although fewer individuals were present in the group, Figure 5.75b indicates some potential separation by sex, with females having the smaller m1L (smaller body sizes) compared to males, with similar m1L to the high latitude wolves. Overall, there is a slight pattern of smaller body sizes at lower latitudes.

However, the more apparent pattern is the separation of sexes, as shown in Figure 5.75b. Across all latitudes examined, males are generally larger than females, based on m1L. Sexual dimorphism in m1L is 6.94% between males and females (see 5.25).

The relationship between m1L (as a proxy for body size) and latitude in males and females was explored using least squares regression (Figure 5.75b). For males, Pearson product moment correlation found the relationship between latitude and m1L to be weakly positive and significant (r_{27} = 0.360, *p*= 0.028). However, the regression was found by ANOVA to be non-significant (F_{28} = 4.017, *p*=0.055), with a non-significant slope (*t*=2.004, *p*=0.055) and low r^2 (r2=0.130) as indicated by Figure 5.75b. This result may account for the low r^2 found in the recent *C. lupus* dataset (Figure 5.75a).

In contrast, for females, the Pearson correlation was strongly positive and significant (r_{20} = 0.783, *p*= 0.0001), and the regression was found by ANOVA to be significant (F_{21} = 31.784, *p*=0.0001), with a significant slope (t=5.638, *p*=0.0001) and higher r^2 (r2=0.614). Thus, male body size is less explained by latitude in comparison to female body size.

To further examine the effect of Bergmann's rule in modern *C. lupus* and because of the relatively small assemblage of lower latitude *C. lupus* available, the Middle Eastern subspecies *C. l. arabs* was included in the dataset (Figure 5.76) for the purpose of extending the latitudinal extent of the wolf.

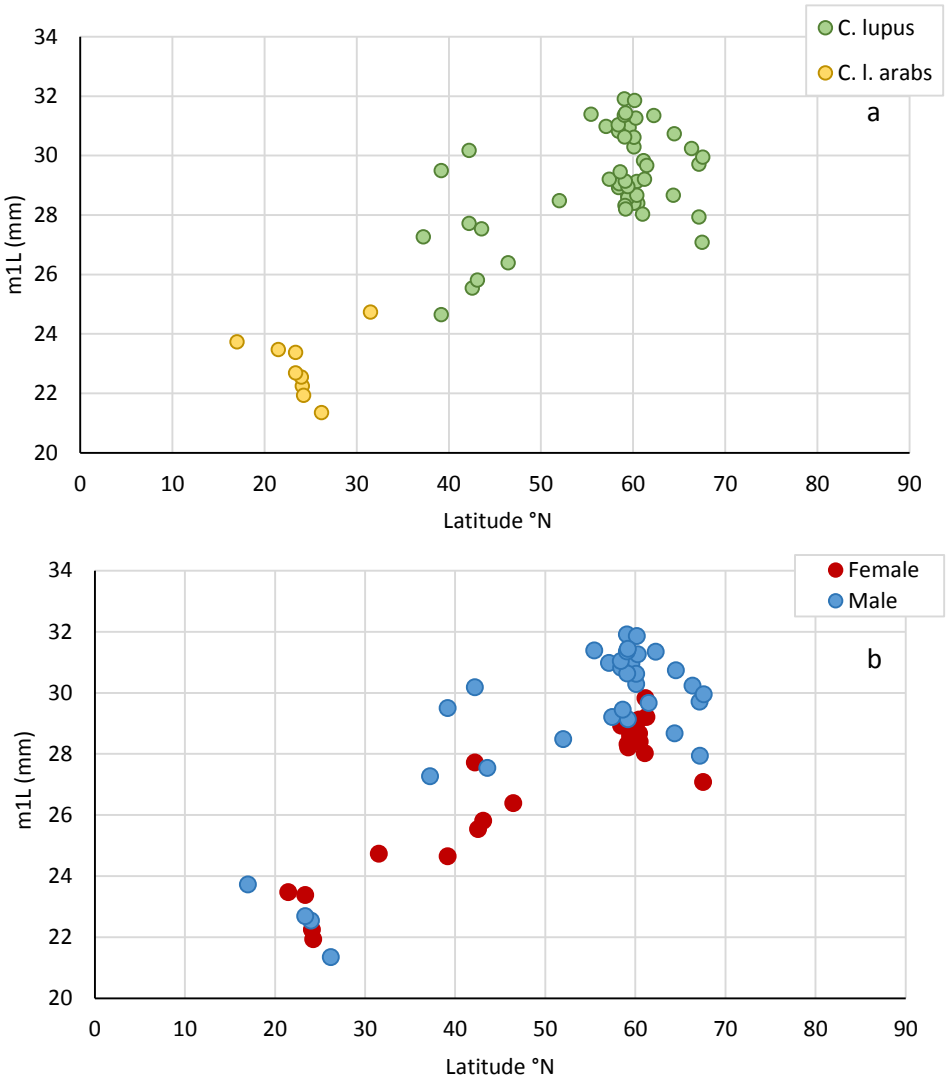


Figure 5.76. Plots showing m1L and latitude for recent European *C. lupus* and Middle Eastern *C. l. arabs*. a). All individuals b). Individuals separated by sex.

The addition of *C. l. arabs* to the modern European *C. lupus* data illustrates well the reduction in body size with increasing lower latitude (Figure 5.76a), albeit in a subspecies of *C. lupus*. However, the apparent separation of body size by sex seen in *C. lupus* is less clear in *C. l. arabs*, with males and females more variable in size rather than separated into discrete clusters, which may relate to the low number of individuals examined (Figure 5.76b).

5.2.7. Bergmann's rule and sexual dimorphism in Pleistocene *C. lupus*

MIS 2, 5a and 6 represent periods of extreme cold climate conditions in Britain. MIS 3, although part of the last glacial cycle, is a period of more variable conditions with rapid alternations between relatively more temperate and colder temperatures. MIS 5e and 7

represent interglacial climates, the former with summer temperatures around 4°C warmer than seen in Britain today and the latter around the same as today (Coope, 2001). As indicated in Table 5.24 and Figure 5.73, the largest estimated body mass for Pleistocene *C. lupus* from Britain is from MIS 5a (39.85 ±1.64Kg). Although the mean estimated body mass for MIS 2 is also large (38.57Kg), there are no associated confidence intervals with it so it cannot be reliably compared with other age groups. In contrast, the reconstruction from MIS 6 (32.18 ±2.70Kg) falls within the range of both the interglacial groups and may reflect a degree of climatic complexity within this long period of overall cold-climate conditions that is obscured by lack of chronological control.

Both MIS 5e and 7 share similar body mass estimates (33.54 ±2.70Kg and 34.03 ±1.73Kg respectively) and are smaller than MIS 5a, with ranges overlapping with MIS 3 (35.40 ±1.63Kg) and 6 (32.18 ±2.70Kg).

C. lupus from Banwell Bone Cave was compared with the high latitude modern *C. lupus* dataset to investigate whether any sexual dimorphism could be detected. Banwell Bone Cave contains the highest number of individuals from one site in this study and since the assemblage is well constrained to MIS 5a, a period of cold-climate conditions, it may be a suitable comparator for modern high latitude wolves. Figure 5.77 illustrates the results.

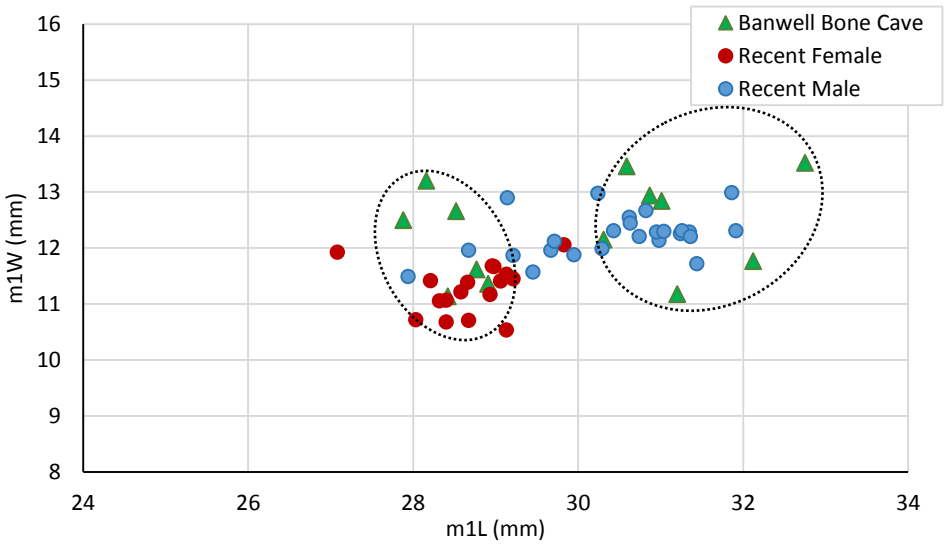


Figure 5.77. Plot showing individual *C. lupus* from Banwell Bone Cave (MIS 5a) against males and females from the modern *C. lupus* high latitude dataset. m1L and m1W used as a body size index. Circles highlight separate Banwell Bone Cave groupings.

Figure 5.77 reveals that Banwell Bone Cave wolves plot in two groups that correspond closely with the clusters of males and females of modern *C. lupus* (highlighted on Figure 5.77). The group with the smallest m1L are all <30mm, whereas the larger group has a

corresponding measurement of >30mm, with one individual having an m1L larger than all recent males. It is therefore possible that the two groups present in the Banwell Bone Cave data do indeed represent males and females.

To test whether significant differences exist between these possible male and female groups at Banwell Bone Cave, a *t* test was used. Differences in male and female mean m1L were found to be significant ($t_{7.84}$ = 7.736, p=0.0001), based on males n=7, mean m1L = 31.69mm, SD = 1.029, and females n=6, mean m1L = 28.44mm, SD = 0.382. Levene's test for equal variances was significant (F_{11} = 10.355, p=0.008), and the *t* test therefore does not assume equality. This result emphasises that the two groups of m1L present at Banwell are significantly different, strongly implying that they may reflect sexual dimorphism between males and females.

t-tests were further used to examine whether the potential Banwell males and females are similar to their recent counterparts. For the all-male group, significant differences were found between modern males and those potentially identified at Banwell (t_{30} = -2.888, p=0.007), based on: males recent n=25, mean m1L = 30.44mm, SD = 1.001, and Banwell males n=7, mean m1L = 31.69mm, SD = 1.029. Levene's test for equal variances was non-significant (F_{30} = 0.090, p=0.767).

In contrast, no difference was found between modern females and the potential Banwell females, with a non-significant result (t_{21} = 0.893, p=0.382), based on: females recent n=17, mean m1L = 28.68mm, SD = 0.606, and Banwell females n=6, mean m1L = 28.44, SD = 0.382. Levene's test for equal variances was non-significant (F_{21} = 0.813, p=0.378).

5.3. Diet

5.3.1. Principal Components Analysis

A Principal Components Analysis (PCA) was carried out on all the cranial raw measurement data, to explore any underlying variation in the dietary measurements. The main Pleistocene canid species examined (*C. lupus*, *C. mosbachensis*, *C. etruscus* and *C. arnensis*) were grouped within a single dataset in order to enable overall variation across all analysed canids. In total, 27 raw measurements were included. Missing values in the analysis were replaced with the mean for that measurement.

5.3.1.1. Analysis

The presence of correlations in the dataset were explored by the PCA, within which correlations of <0.9 and >0.1 are preferred, as either overly high correlation (and hence linearity) or low correlation between measurements may cause loading on to only one principal component (PC). Since a strong linear relationship between m1L and m1W was previously identified in Section 5.1, both measurements were removed from the PCA.

The presence of complexity in some measurements was also initially identified by the rotated component matrix. Complex measurements here load highly onto more than one PC. For the canid dataset, m1Ltrig, m1Ltal, m2L, m2W, p1p4L, m1m2D, m1m2B, P4L were all complex. These measurements were consequently also removed from the PCA, in order to provide the simplest explanation of variation within the canid dataset.

The revised canid raw measurement dataset was then tested for its suitability for use in a PCA. The revised correlation matrix indicated that the correlations between the measurements were now appropriate. The determinant of correlation for the correlation matrix was (0.00000652) >0, and hence indicated no linear dependencies.

The Kaiser-Meyer-Olkin Measure (KMO) of sampling adequacy and Bartlett's Test of Sphericity were included in the analysis to gauge the suitability and quality of the dataset, and hence establish whether a PCA would be useful for the dataset.

The KMO measure indicates the proportion of variance present in the measurements. A KMO <0.5 suggests data is inappropriate for a PCA. The KMO for the dataset was 0.894 and was therefore judged to be satisfactory for application of PCA.

The Bartlett's Test of Sphericity tests whether the measurements are unrelated and thus unsuitable for use with a PCA. The Bartlett's Test was significant (χ_2 = 544.552, p=0.0001) indicating that strong relationships exist between the measurements and that the revised canid dataset is suitable for a PCA.

The communalities (i.e. the variance in observed variables accounted for by common factors) shown in Table 5.35 indicate the proportion of variance in each measurement that can be accounted for by the PCs present.

	Initial	Extraction
p4L	1.000	.874
p4W	1.000	.868
p2p4L	1.000	.644
p1m3L	1.000	.729
p2m3L	1.000	.670
p3p4D	1.000	.799
p3p4B	1.000	.670
UP3L	1.000	.471
UP4W	1.000	.697
UM1L	1.000	.599
UM1W	1.000	.722
UM2W	1.000	.626
DentaryL	1.000	.553
UP1P4L	1.000	.689
UP1M2L	1.000	.566
UC1M2L	1.000	.613
UM1M2L	1.000	.618

Table 5.35. Communalities of the revised canid dataset for PCA. Measurements indicating the proportion of variance within each measurement.

Initial communalities are estimates of variation in each measurement accounted for by the components. In a PCA these equal 1. Of note are the extraction communalities, which represent estimates of variation in each measurement (variable) that can be explained by the PCs. Communalities with low values may be problematic in the analysis as they do not represent high enough variation. All communalities are above the minimum value (<0.4), indicating suitably high variation is present.

Table 5.36 shows the total variance explained in the PCA. Four principal components (PC) were extracted by the analysis, indicated by eigenvalues >1.

	Initial Eigenvalues			Extraction Sums of Squared Loadings			Rotation Sums of Squared Loadings		
Component	Total	% Var	Cumulative %	Total	% Var	Cumulative %	Total	% Var	Cumulative %
1	7.401	43.533	43.533	7.401	43.533	43.533	3.426	20.156	20.156
2	1.883	11.079	54.612	1.883	11.079	54.612	3.389	19.937	40.093
3	1.094	6.435	61.047	1.094	6.435	61.047	2.591	15.243	55.336
4	1.029	6.051	67.098	1.029	6.051	67.098	2.000	11.762	67.098

5	.827	4.864	71.962						
6	.663	3.901	75.863						
7	.633	3.722	79.585						
8	.549	3.228	82.812						
9	.516	3.034	85.846						
10	.425	2.501	88.347						
11	.422	2.482	90.830						
12	.369	2.170	93.000						
13	.329	1.936	94.936						
14	.274	1.610	96.546						
15	.234	1.379	97.925						
16	.205	1.206	99.132						
17	.148	.868	100.000						

Table 5.36. Results from the PCA of revised canid measurements. Eigenvalues and total variance explained are shown.

PC 1 accounts for the largest amount of variation in the dataset (43.53%), followed by PC 2 (11.07%). All together, the four extracted components explain 67.10% of the variance in the dataset.

The rotated component matrix indicates the component loadings, which represent the correlations between each measurement and the extracted PCs. Varimax orthogonal rotation was used to simplify the component loadings, and thus create the simplest structure in the dataset. Table 5.37 shows the component loadings for the revised canid dataset.

	Component			
	1	2	3	4
p4L	.250	.233	.116	**.862**
p4W	.216	.350	.083	**.832**
p2p4L	.032	**.701**	.173	.348
p1m3L	**.763**	.181	.261	.214
p2m3L	**.604**	.313	.296	.345
p3p4D	.190	**.820**	.109	.279
p3p4B	.288	**.736**	.105	.187
UP3L	**.581**	.346	.065	.099
UP4W	**.648**	.327	.358	.206
UM1L	.371	**.647**	.102	.179
UM1W	.349	**.766**	.110	-.035
UM2W	**.704**	.237	.194	.193
DentaryL	.285	.211	**.653**	-.019
UP1P4L	.088	.161	**.809**	.020
UP1M2L	.263	.007	**.700**	.085
UC1M2L	.169	.059	**.740**	.184
UM1M2L	**.742**	.120	.228	.018

Table 5.37. Results from the rotated component loadings using Varimax with Kaiser normalisation. Rotation converged in 7 iterations. Measurements with highest loadings shown in bold.

After the removal of complexly loading measurements as described earlier, all measurements now load highly on to one of the four PCs (Table 5.37). The measurements most highly correlated with PC1 are p1m3L, M1M2L, M2W, P4W, p2m3L, P3L, whereas the measurements most highly correlated with PC2 are M1W, p3p4D, p3p4B, p2p4L, M1L. PC 3 and 4 only account for 6% of the variation each. P1P4L, C1M2L, P1M2L and DentaryL are correlated with PC3, whereas p4L and p4W are correlated with PC4.

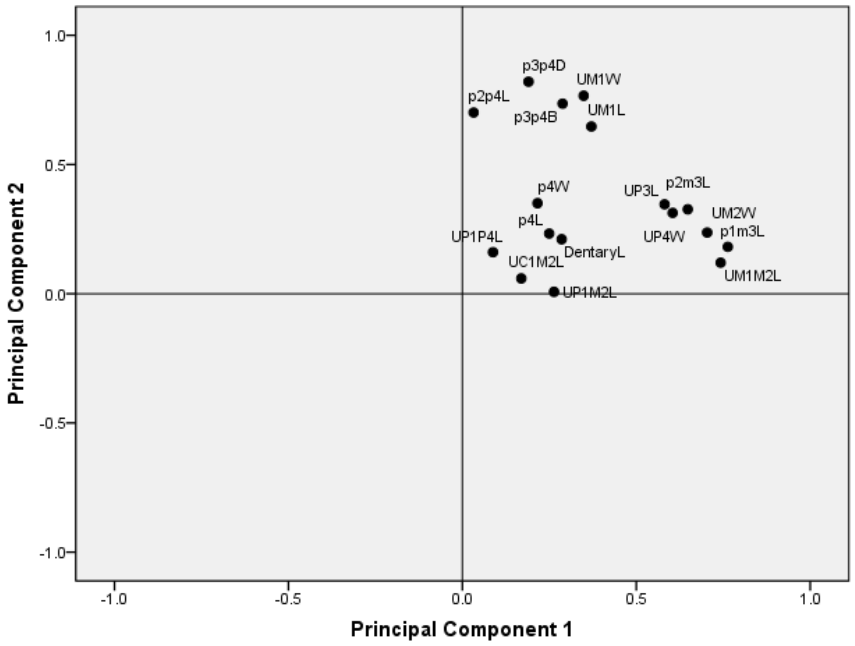


Figure 5.78. Biplot of the rotated component loadings of each measurement on principal components 1 and 2 for the revised canid dataset.

Figure 5.78 illustrates the measurement loadings onto the main principal components. The strong relationships between the measurements and both PCs are exemplified by the positive loadings.

The ability of the four extracted PCs to explain the underlying variation in the canid dataset can be tested by reproducing the correlations in the original correlation matrix using the extracted components. The reproduced correlations found 47 non-redundant residuals (34%) that had absolute values greater than 0.05. This value is below 50%, which is used as a standard to measure the success of the reproduction. Hence, the four principal components are successfully representing the variation present in the original dataset.

To summarise, the PCA extracted four PCs that explained the variation in the revised canid dataset. PC 1 explained the highest amount of variation, with p1m3L, M1M2L, M2W, P4W, p2m3L, P3L all highly correlated. Whilst on PC 2, M1W, p3p4D, p3p4B, p2p4L, M1L were highly correlated, although this component explained less variation than PC1.

From the PCA it is evident that lower tooth row lengths, upper molar crushing area, upper carnassial width and mandible breadth and depth at the p3-p4 junction (as a proxy for jaw strength) are responsible for the most variation in the dataset.

The removal of measurements due to linearity (m1L, m1W) and complexity (m1Ltrig, m1Ltal, m2L, m2W, p1p4L, m1m2D, m1m2B, P4L), however, limited the scope of the PCA, with possible variation within these measurements not fully explored. In light of this, all measurements were analysed using further univariate and multivariate statistical methods shown in the following sections.

5.3.2. Temporal analysis of dietary measurements

The presence of temporal variation was examined for all canids (where applicable) from Britain and mainland Europe using one-way ANOVA (for >2 samples) and *t* tests (for 2 samples). As explained in Chapter 4, criteria for using both tests relies on assumptions that data are independent, normally distributed, and have homogeneous variance. However, as some of the following analyses contain small sample sizes, it is important to note that in ANOVA this can cause increased vulnerability to violations in test assumptions, typically in the homogeneity of variance. Hence, although ANOVA is a robust test, small sample sizes can increase the risk of type I errors as sample size affects homogeneity of variance most (Zar, 2010), making tests for homogeneity of variance essential (Sokal and Rohlf, 1995).

However, there is no simple answer to how large a sample must be for analysis (Sokal and Rohlf, 1995), and unfortunately small sample sizes in palaeontological analyses are often unavoidable, making sample size issues difficult to rectify. Although non-parametric tests are generally less affected by assumption violations and can be used if sample size cannot be increased (Sokal and Rohlf, 1995), these tests are of comparatively lower overall power, especially when parametric assumptions are met (Sokal and Rohlf, 1995). Here only parametric tests were used as data are considered independent and normally distributed (see 5.1), and Levene's test was employed alongside both ANOVA and *t* tests to assess homogeneity of variance.

Following Sokal and Rohlf (1995), if variances were found homogeneous, then the use of ANOVA is justified. Also, if however variances are moderately heterogeneous, the consequences are not too serious for overall test significance, although it is important to note that comparisons with single degree-of-freedom may be far from accurate (Sokal and Rohlf, 1995). Thus, it is possible to include small sample sizes in tests of variance, as long as errors are understood and accommodated for.

5.3.2.1. Temporal analysis: *C. lupus* from Britain

To investigate the presence of temporal variation in Pleistocene *C. lupus* from Britain, one-way ANOVA was employed. Homogeneity of variance was assessed using Levene's test alongside the one-way ANOVA.

Although assemblages were available from most MIS age groups with *C. lupus*, these were frequently represented by fewer than four individuals. Therefore age groups containing the highest number of individuals (MIS 3, 5a and 7) were analysed using one-way ANOVA to examine the presence of temporal variation. Table 5.38 indicates the results from Levene's test and one-way ANOVA.

Measure	MIS	n	mean	SD	Levene's test	one-way ANOVA
p4L	3	17	16.14	0.674	$F_{(2, 50)} = 0.652$, $p=0.526$	$F_{(2, 50)} = 6.291$, $p=0.004$
	5a	29	16.90	0.832		
	7	7	16.12	0.856		
	Total	53	16.55	0.856		
p4W	3	17	8.22	0.474	$F_{(2, 50)} = 1.091$, $p=0.344$	$F_{(2, 50)} = 4.375$, $p=0.018$
	5a	29	8.63	0.604		
	7	7	8.01	0.827		
	Total	53	8.41	0.636		
m1Ltrig	3	20	20.66	1.201	$F_{(2, 44)} = 0.039$, $p=0.962$	$F_{(2, 44)} = 5.784$, $p=0.006$
	5a	18	21.64	1.103		
	7	9	20.14	1.268		
	Total	47	20.93	1.294		
m1Ltal	3	19	7.34	0.544	$F_{(2, 43)} = 1.453$, $p=0.245$	$F_{(2, 43)} = 0.526$, $p=0.595$
	5a	18	7.56	0.624		
	7	9	7.51	0.911		
	Total	46	7.46	0.650		
m1W	3	20	11.68	0.649	$F_{(2, 44)} = 0.669$, $p=0.518$	$F_{(2, 44)} = 9.920$, $p=0.0001$
	5a	18	12.38	0.761		
	7	9	11.18	0.678		
	Total	47	11.85	0.824		
m2L	3	17	11.56	0.574	$F_{(2, 41)} = 2.385$, $p=0.105$	$F_{(2, 41)} = 1.840$, $p=0.172$
	5a	17	11.55	0.851		
	7	10	11.00	1.026		
	Total	44	11.43	0.817		
m2W	3	16	8.68	0.514	$F_{(2, 39)} = 2.239$,	$F_{(2, 39)} = 2.274$,

	5a	16	8.91	0.714	*p*=0.120	*p*=0.116
	7	10	8.31	0.907		
	Total	42	8.68	0.719		
p1p4L	3	11	50.74	3.227	$F_{(2, 26)} = 3.371$, *p*=0.050	$F_{(2, 26)} = 0.086$, *p*=0.917
	5a	13	50.90	2.155		
	7	5	50.34	1.411		
	Total	29	50.74	2.457		
p2p4L	3	12	44.86	2.917	$F_{(2, 28)} = 3.240$, *p*=0.054	$F_{(2, 28)} = 0.503$, *p*=0.610
	5a	14	44.38	2.022		
	7	5	43.63	1.075		
	Total	31	44.44	0.411		
p1m3L	3	7	96.59	3.953	$F_{(2, 14)} = 0.512$, *p*=0.610	$F_{(2, 14)} = 1.175$, *p*=0.338
	5a	6	96.64	4.492		
	7	4	93.18	2.615		
	Total	17	95.81	3.963		
p2m3L	3	8	90.18	4.087	$F_{(2, 15)} = 0.059$, *p*=0.943	$F_{(2, 15)} = 0.385$, *p*=0.687
	5a	6	90.30	3.874		
	7	4	88.17	4.755		
	Total	18	89.77	4.008		
DentaryL	3	2	165.50	6.364	$F_{(2, 3)} = 5.077\text{^}15$, *p*=0.0001	$F_{(2, 3)} = 0.283$, *p*=0.772
	5a	2	168.50	10.607		
	7	2	163.00	2.828		
	Total	6	165.67	6.186		
p3p4D	3	12	27.82	1.350	$F_{(2, 30)} = 0.924$, *p*=0.408	$F_{(2, 30)} = 3.376$, *p*=0.048
	5a	15	27.75	1.439		
	7	6	25.83	2.631		
	Total	33	27.43	1.790		
p3p4B	3	12	12.45	0.864	$F_{(2, 27)} = 1.781$, *p*=0.188	$F_{(2, 27)} = 6.220$, *p*=0.006
	5a	12	13.47	1.643		
	7	6	11.33	0.835		
	Total	30	12.63	1.444		
m1m2D	3	9	30.77	2.499	$F_{(2, 30)} = 0.832$, *p*=0.445	$F_{(2, 30)} = 3.219$, *p*=0.054
	5a	17	31.80	2.241		
	7	7	29.29	1.731		
	Total	33	30.99	2.372		
m1m2B	3	9	12.93	1.568	$F_{(2, 28)} = 1.945$, *p*=0.162	$F_{(2, 28)} = 8.508$, *p*=0.001
	5a	14	13.88	1.102		
	7	8	11.73	0.252		
	Total	31	13.05	0.260		
P3L	3	11	16.08	1.266	$F_{(2, 26)} = 0.522$, *p*=0.599	$F_{(2, 26)} = 0.473$, *p*=0.628
	5a	13	16.48	1.134		
	7	5	16.04	0.817		
	Total	29	16.25	1.124		
P4L	3	6	25.57	0.844	$F_{(2, 15)} = 1.817$, *p*=0.197	$F_{(2, 15)} = 0.806$, *p*=0.465
	5a	10	26.22	1.647		
	7	2	24.90	2.411		
	Total	18	25.85	1.484		
P4W	3	6	13.42	1.826	$F_{(2, 15)} = 1.297$, *p*=0.302	$F_{(2, 15)} = 0.375$, *p*=0.694
	5a	10	13.35	1.172		
	7	2	14.29	1.032		
	Total	18	13.48	1.363		
M1L	3	13	15.97	1.264	$F_{(2, 36)} = 0.670$, *p*=0.518	$F_{(2, 36)} = 0.529$, *p*=0.594
	5a	18	16.24	0.899		
	7	8	15.83	0.838		

	Total	39	16.07	1.013		
M1W	3	12	22.58	1.972	$F_{(2, 32)} = 1.689$, $p=0.201$	$F_{(2, 32)} = 2.932$, $p=0.068$
	5a	17	21.35	0.972		
	7	6	21.54	0.768		
	Total	35	21.80	1.455		
M2W	3	4	13.82	0.789	$F_{(2, 15)} = 0.094$, $p=0.911$	$F_{(2, 15)} = 0.287$, $p=0.755$
	5a	9	13.57	0.834		
	7	5	13.39	0.863		
	Total	18	13.58	0.797		
P1P4L	N/A					
P1M2L	N/A					
C1M2L	N/A					
M1M2L	3	5	21.80	2.630	$F_{(2, 16)} = 2.705$, $p=0.097$	$F_{(2, 16)} = 0.894$, $p=0.428$
	5a	10	22.95	1.54		
	7	4	21.86	1.316		
	Total	19	22.42	1.830		

Table 5.38. Results from one-way ANOVA for temporal analysis (MIS 3, 5a and 7) of *C. lupus* from Britain. Results include number, mean and standard deviation for each age group, result from Levene's test of equal variances, and result of one-way ANOVA for each measurement. Significant result indicated by $p<0.05$.

- Levene's test found DentaryL significant, indicating unequal variance and possibly relating to small sample size. As this measurement had normal distribution and independence, the violation of homogeneous variances was of minimal concern and the ANOVA result was retained.
- Levene's test found remaining measurements as non-significant, indicating equal variances.
- One-way ANOVA found p4L, p4W, m1Ltrig, m1W, p3p4D, p3p4B, m1m2B to be significant. m1m2D had suggestive significance ($p=0.054$). *Post hoc* tests were subsequently employed to investigate the cause of the significance.
- The remaining measurements (m1Ltal, m2L, m2W, p1p4L, p2p4L, p1m3L, DentaryL, P3L, P4L, P4W, M1L, M1W, M2W, and M1M2L) were non-significant, indicating that no temporal variation was present, and thus were not analysed further.

The significant measurements (Table 5.38) were further analysed by Tukey Honestly Significant Difference (HSD) *post hoc* test, enabling multiple comparisons between age groups. Table 5.39 shows the results for p4L between MIS 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
3	5a	-.75613*	.23828	.007	-1.3317	-.1806
	7	.02496	.35032	.997	-.8212	.8711
5a	3	.75613*	.23828	.007	.1806	1.3317
	7	.78108	.32850	.055	-.0124	1.5746
7	3	-.02496	.35032	.997	-.8711	.8212
	5a	-.78108	.32850	.055	-1.5746	.0124

Table 5.39. Results of *post hoc* tests for one way ANOVA using Tukey HSD for p4L in MIS 3, 5a and 7. Mean difference is significance at 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 3 and 5a.
- Pairings of MIS 3 and MIS 7, and MIS 5a and MIS 7 were non-significant and similar.

Table 5.40 shows the results of *post hoc* one way ANOVA using Tukey HSD for p4W between MIS 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
3	5a	-.40974	.18287	.074	-.8514	.0320
	7	.21076	.26885	.715	-.4386	.8601
5a	3	.40974	.18287	.074	-.0320	.8514
	7	.62049*	.25211	.045	.0115	1.2294
7	3	-.21076	.26885	.715	-.8601	.4386
	5a	-.62049*	.25211	.045	-1.2294	-.0115

Table 5.40. Results of *post hoc* one way ANOVA using Tukey HSD for p4W in MIS 3, 5a and 7. Mean difference is significance at 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 5a and 7.
- MIS 3 and 5a, and MIS 3 and 7 were non-significant.

Table 5.41 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of m1Ltrig between MIS 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
3	5a	-.97961*	.38239	.036	-1.9071	-.0521
	7	.51206	.47242	.529	-.6338	1.6579
5a	3	.97961*	.38239	.036	.0521	1.9071
	7	1.49167*	.48050	.009	.3262	2.6571
7	3	-.51206	.47242	.529	-1.6579	.6338
	5a	-1.49167*	.48050	.009	-2.6571	-.3262

Table 5.41. Results of *post hoc* one way ANOVA using Tukey HSD for m1Ltrig in MIS 3, 5a and 7. Mean difference is significance at 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 3 and 5a, and MIS 5a and 7.
- MIS 3 and 7 were non-significant.

Table 5.42 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of m1W between MIS 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
3	5a	-.70228*	.22721	.009	-1.2534	-.1512
	7	.49883	.28071	.189	-.1820	1.1797

5a	3	.70228*	.22721	.009	.1512	1.2534
	7	1.20111*	.28551	.000	.5086	1.8936
7	3	-.49883	.28071	.189	-1.1797	.1820
	5a	-1.20111*	.28551	.000	-1.8936	-.5086

Table 5.42. Results of *post hoc* one way ANOVA using Tukey HSD for m1W in MIS 3, 5a and 7. Mean difference is significance at 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 3 and 5a and MIS 5a and 7.
- MIS 3 and 7 were found to be non-significant.

Table 5.43 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of p3p4D between MIS 3, 5a and 7.

					95% Confidence Interval	
MIS	**MIS**	**Mean Difference**	**Std. Error**	**Sig.**	**Lower Bound**	**Upper Bound**
3	5a	.07017	.64677	.994	-1.5243	1.6646
	7	1.99583	.83497	.059	-.0626	4.0543
5a	3	-.07017	.64677	.994	-1.6646	1.5243
	7	1.92567	.80666	.059	-.0630	3.9143
7	3	-1.99583	.83497	.059	-4.0543	.0626
	5a	-1.92567	.80666	.059	-3.9143	.0630

Table 5.43. Results of *post hoc* one way ANOVA using Tukey HSD for p3p4D in MIS 3, 5a and 7. Mean difference is significance at 0.05 level. Significant result indicated by $p<0.05$.

- This significance was not replicated by the *post hoc* tests. All comparisons were non-significant.

Table 5.44 shows the results of *post hoc* one-way ANOVA using Tukey HSD for multiple comparisons of p3p4B between MIS 3, 5a and 7.

					95% Confidence Interval	
MIS	**MIS**	**Mean Difference**	**Std. Error**	**Sig.**	**Lower Bound**	**Upper Bound**
3	5a	-1.02500	.50547	.125	-2.2783	.2283
	7	1.11833	.61908	.187	-.4166	2.6533
5a	3	1.02500	.50547	.125	-.2283	2.2783
	7	2.14333*	.61908	.005	.6084	3.6783
7	3	-1.11833	.61908	.187	-2.6533	.4166
	5a	-2.14333*	.61908	.005	-3.6783	-.6084

Table 5.44. Results of *post hoc* one way ANOVA using Tukey HSD for p3p4B in MIS 3, 5a and 7. Mean difference is significance at 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 5a and 7.
- MIS 3 with both MIS 5a and 7 were non-significant.

Table 5.45 shows the results of *post hoc* one-way ANOVA using Tukey HSD for multiple comparisons of m1m2D between MIS 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
3	5a	-1.03111	.91652	.506	-3.2906	1.2284
	7	1.47889	1.12045	.395	-1.2833	4.2411
5a	3	1.03111	.91652	.506	-1.2284	3.2906
	7	2.51000*	.99847	.045	.0485	4.9715
7	3	-1.47889	1.12045	.395	-4.2411	1.2833
	5a	-2.51000*	.99847	.045	-4.9715	-.0485

Table 5.45. Results of *post hoc* one way ANOVA using Tukey HSD for m1m2D in MIS 3, 5a and 7. Mean difference is significance at 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 5a and 7.
- MIS 3 and 5a, and MIS 3 and 7 were non-significant.

Table 5.46 shows the results of *post hoc* one-way ANOVA using Tukey HSD for multiple comparisons of m1m2B between MIS 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
3	5a	-.94746	.50428	.164	-2.1952	.3003
	7	1.20236	.57353	.109	-.2167	2.6215
5a	3	.94746	.50428	.164	-.3003	2.1952
	7	2.14982*	.52312	.001	.8554	3.4442
7	3	-1.20236	.57353	.109	-2.6215	.2167
	5a	-2.14982*	.52312	.001	-3.4442	-.8554

Table 5.46. Results of *post hoc* one way ANOVA using Tukey HSD for m1m2B in MIS 3, 5a and 7. Mean difference is significance at 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 5a and 7.
- Pairings of MIS 3 and 5a, and MIS 3 and 7 were non-significant.

Summary

Only age groupings with a consistently high enough number of individuals could be analysed by one-way ANOVA. Nonetheless, small sample sizes were present for some measurements, particularly of MIS 7 age. Levene's test found the majority of measurements as having homogeneous variances. Measurements found to be temporally significant include p4L, p4W, m1Ltrig, m1W, p3p4B, m1m2D and m1m2B, which were further analysed by *post hoc* tests using Tukey HSD for multiple comparisons between age groups. As a result, p4L was significant between MIS 3 and 5a only. m1Ltrig and m1W were significant between MIS 3 and 5a, and MIS 5a and 7. In contrast, p3p4B and m1m2B were only significant between MIS 5a and 7. Both p4W (p=0.045) and m1m2D (p=0.045) were found to be significant between MIS 5a and 7. All measurements were found to be similar between the MIS 3 and 7 groupings.

5.3.2.1.1. Temporal analysis: *C. lupus* from Britain with the modern Swedish wolf group

As the modern all-European *C. lupus* dataset may contain variation related to latitude, a discrete sub-set of modern *C. lupus* from central and northern Sweden was analysed alongside the Pleistocene age groups. Table 5.47 indicates the results of one-way ANOVA between modern (MIS 1), MIS 3, 5a and 7 *C. lupus*.

Measure	MIS	n	mean	SD	Levene's test	one-way ANOVA
p4L	1	42	15.58	0.106	$F_{(3, 91)} = 0.723$, $p=0.541$	$F_{(3, 91)} = 18.154$, $p=0.0001$
	3	17	16.14	0.164		
	5a	29	16.90	0.155		
	7	7	16.12	0.299		
	Total	95	16.12	0.094		
p4W	1	42	8.10	0.563	$F_{(3, 91)} = 0.786$, $p=0.505$	$F_{(3, 91)} = 5.396$, $p=0.002$
	3	17	8.22	0.474		
	5a	29	8.63	0.604		
	7	7	8.01	0.827		
	Total	95	8.27	0.622		
m1Ltrig	1	42	20.49	0.928	$F_{(3, 85)} = 0.514$, $p=0.674$	$F_{(3, 85)} = 6.027$, $p=0.001$
	3	20	20.66	1.201		
	5a	18	21.64	1.103		
	7	9	20.14	1.268		
	Total	89	20.72	1.152		
m1Ltal	1	42	7.93	0.570	$F_{(3, 84)} = 1.283$, $p=0.286$	$F_{(3, 84)} = 4.733$, $p=0.004$
	3	19	7.34	0.544		
	5a	18	7.56	0.624		
	7	9	7.51	0.911		
	Total	88	7.68	0.655		
m1W	1	42	11.84	0.625	$F_{(3, 85)} = 0.555$, $p=0.0.646$	$F_{(3, 85)} = 7.329$, $p=0.0001$
	3	20	11.68	0.649		
	5a	18	12.38	0.761		
	7	9	11.18	0.679		
	Total	89	11.85	0.733		
m2L	1	42	12.11	0.689	$F_{(3, 82)} = 1.948$, $p=0.128$	$F_{(3, 82)} = 7.327$, $p=0.0001$
	3	17	11.56	0.574		
	5a	17	11.55	0.851		
	7	10	11.00	1.026		
	Total	86	11.76	0.827		
m2W	1	42	9.17	0.434	$F_{(3, 80)} = 4.198$, $p=0.008$	$F_{(3, 80)} = 7.202$, $p=0.0001$
	3	16	8.68	0.514		
	5a	16	8.91	0.714		
	7	10	8.31	0.907		
	Total	84	8.92	0.640		
p1p4L	1	41	50.28	2.391	$F_{(3, 66)} = 1.736$, $p=0.168$	$F_{(3, 66)} = 0.265$, $p=0.851$
	3	11	50.74	3.227		
	5a	13	50.90	2.155		
	7	5	50.34	1.411		
	Total	70	50.47	2.411		
p2p4L	1	42	43.40	1.758	$F_{(3, 69)} = 3.435$, $p=0.022$	$F_{(3, 69)} = 2.054$, $p=0.114$
	3	12	44.86	2.917		
	5a	14	44.37	2.022		
	7	5	43.63	1.075		

	Total	73	43.84	2.051		
p1m3L	1	42	96.08	2.769	$F_{(3, 55)} = 1.194$, $p=0.321$	$F_{(3, 55)} = 1.281$, $p=0.290$
	3	7	96.59	3.953		
	5a	6	96.64	4.492		
	7	4	93.18	2.615		
	Total	59	96.00	3.125		
p2m3L	1	42	89.45	2.678	$F_{(3, 56)} = 1.795$, $p=0.159$	$F_{(3, 56)} = 0.493$, $p=0.689$
	3	8	90.18	4.087		
	5a	6	90.30	3.874		
	7	4	88.17	4.755		
	Total	60	89.55	3.104		
DentaryL	1	43	178.09	8.412	$F_{(3, 45)} = 0.682$, $p=0.568$	$F_{(3, 45)} = 4.038$, $p=0.013$
	3	2	165.50	6.364		
	5a	2	168.50	10.601		
	7	2	163.00	2.828		
	Total	49	176.57	9.101		
p3p4D	1	42	28.56	2.105	$F_{(3, 71)} = 2.264$, $p=0.088$	$F_{(3, 71)} = 3.787$, $p=0.014$
	3	12	27.82	1.350		
	5a	15	27.75	1.439		
	7	6	25.83	2.631		
	Total	75	28.06	2.040		
p3p4B	1	42	13.11	1.133	$F_{(3, 68)} = 1.403$, $p=0.249$	$F_{(3, 68)} = 5.560$, $p=0.002$
	3	12	12.45	0.864		
	5a	12	13.47	1.643		
	7	6	11.33	0.835		
	Total	72	12.91	1.284		
m1m2D	1	42	34.03	2.410	$F_{(3, 71)} = 0.610$, $p=0.611$	$F_{(3, 71)} = 12.441$, $p=0.0001$
	3	9	30.77	2.499		
	5a	17	31.80	2.241		
	7	7	29.29	1.731		
	Total	75	32.69	2.822		
m1m2B	1	42	13.12	1.156	$F_{(3, 69)} = 1.166$, $p=0.329$	$F_{(3, 69)} = 5.831$, $p=0.001$
	3	9	12.93	1.568		
	5a	14	13.88	1.102		
	7	8	11.73	0.713		
	Total	73	13.09	1.278		
P3L	1	41	16.02	0.884	$F_{(3, 65)} = 0.762$, $p=0.519$	$F_{(3, 65)} = 0.911$, $p=0.441$
	3	10	15.90	1.166		
	5a	13	16.48	1.134		
	7	5	16.04	0.817		
	Total	69	16.09	0.972		
P4L	1	42	26.61	1.154	$F_{(3, 56)} = 1.934$, $p=0.135$	$F_{(3, 56)} = 2.309$, $p=0.086$
	3	6	25.57	0.844		
	5a	10	26.22	1.647		
	7	2	24.90	2.411		
	Total	60	26.39	1.298		
P4W	1	42	14.45	0.977	$F_{(3, 56)} = 2.225$, $p=0.095$	$F_{(3, 56)} = 3.620$, $p=0.018$
	3	6	13.42	1.826		
	5a	10	13.35	1.172		
	7	2	14.29	1.032		
	Total	60	14.16	1.183		
M1L	1	43	17.27	0.787	$F_{(3, 78)} = 0.802$, $p=0.496$	$F_{(3, 78)} = 12.415$, $p=0.0001$
	3	13	15.97	1.264		
	5a	18	16.24	0.900		

	7	8	15.83	0.838		
	Total	82	16.70	1.079		
M1W	1	43	23.23	1.202	$F_{(3, 74)} = 1.667$, $p=0.181$	$F_{(3, 74)} = 10.163$, $p=0.0001$
	3	12	22.58	1.972		
	5a	17	21.35	0.972		
	7	6	21.54	0.768		
	Total	78	22.59	1.493		
M2W	1	42	14.48	0.700	$F_{(3, 56)} = 0.106$, $p=0.956$	$F_{(3, 56)} = 6.577$, $p=0.001$
	3	4	13.82	0.789		
	5a	9	13.57	0.834		
	7	5	13.39	0.863		
	Total	60	14.21	0.836		
P1P4L	N/A					
P1M2L	N/A					
C1M2L	N/A					
M1M2L	1	43	24.07	1.085	$F_{(3, 58)} = 5.605$, $p=0.002$	$F_{(3, 58)} = 7.852$, $p=0.0001$
	3	5	21.80	2.630		
	5a	10	22.95	1.541		
	7	4	21.86	1.316		
	Total	62	23.57	1.546		

Table 5.47. Results from Levene's test and one-way ANOVA for temporal analysis of age groups MIS 1, 3, 5a and 7 containing modern *C. lupus* from Sweden (MIS 1) and Pleistocene *C. lupus* from Britain. Significant result indicated by $p<0.05$.

- Levene's test found m2W, p2p4L, and M1M2L significant, indicating unequal variances. As all measurements were normally distributed and from independent samples, the violation of homogeneous variances was of minimal concern and the ANOVA result was retained.
- Levene's test found the remaining measurements as non-significant, indicating equal variances.
- One-way ANOVA found p4L, p4W, m1Ltrig, m1Ltal, m1W, m2L, m2W, DentaryL, p3p4D, p3p4B, m1m2D, m1m2B, P4W, M1L, M1W, M2W and M1M2L to be significant, indicating temporal differences present between the age groups.

In the previous analysis of MIS 3, 5a and 7, only p4L, m1Ltrig, m1W, p3p4B, m1m2D and m1m2B were found to be significant, indicating further differences between the Pleistocene groups and recent Swedish wolves. The remaining measurements were non-significant and hence similar between the age groups.

The measurements found to be significant (Table 5.47) were further analysed by *post hoc* tests for one-way ANOVA, using Tukey HSD to allow for multiple comparisons. Table 5.48 shows the results for p4L between MIS 1 (modern), MIS 3, 5a and 7, focussing on differences with the modern MIS 1 group.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	-.56186*	.21266	.047	-1.1184	-.0053
	5a	-1.31799*	.17862	.000	-1.7855	-.8505
	7	-.53690	.30202	.291	-1.3273	.2535
3	1	.56186*	.21266	.047	.0053	1.1184
	5a	-.75613*	.22598	.006	-1.3476	-.1647
	7	.02496	.33224	1.000	-.8446	.8945
5a	1	1.31799*	.17862	.000	.8505	1.7855
	3	.75613*	.22598	.006	.1647	1.3476
	7	.78108	.31155	.065	-.0343	1.5964
7	1	.53690	.30202	.291	-.2535	1.3273
	3	-.02496	.33224	1.000	-.8945	.8446
	5a	-.78108	.31155	.065	-1.5964	.0343

Table 5.48. Results of *post hoc* one way ANOVA using Tukey HSD for p4L in MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 1 and 5a, and suggestive significance between MIS 1 and 3 ($p=0.47$).
- MIS 1 with both MIS 3 and 7 were non-significant.

Table 5.49 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of P4W between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	-.12123	.16755	.887	-.5597	.3173
	5a	-.53097*	.14073	.002	-.8993	-.1627
	7	.08952	.23796	.982	-.5332	.7123
3	1	.12123	.16755	.887	-.3173	.5597
	5a	-.40974	.17804	.105	-.8757	.0562
	7	.21076	.26176	.852	-.4743	.8958
5a	1	.53097*	.14073	.002	.1627	.8993
	3	.40974	.17804	.105	-.0562	.8757
	7	.62049	.24546	.062	-.0219	1.2629
7	1	-.08952	.23796	.982	-.7123	.5332
	3	-.21076	.26176	.852	-.8958	.4743
	5a	-.62049	.24546	.062	-1.2629	.0219

Table 5.49. Results of *post hoc* one way ANOVA using Tukey HSD for p4W in MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 1 and 5a.
- MIS 1 with both MIS 3 and 7 were non-significant, indicating similarity.

Table 5.50 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of m1Ltrig between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	-.17126	.28917	.934	-.9291	.5865

	5a	-1.15087*	.29985	.001	-1.9367	-.3651
	7	.34079	.39096	.819	-.6838	1.3653
3	1	.17126	.28917	.934	-.5865	.9291
	5a	-.97961*	.34581	.029	-1.8858	-.0734
	7	.51206	.42723	.629	-.6075	1.6316
5a	1	1.15087*	.29985	.001	.3651	1.9367
	3	.97961*	.34581	.029	.0734	1.8858
	7	1.49167*	.43453	.005	.3529	2.6304
7	1	-.34079	.39096	.819	-1.3653	.6838
	3	-.51206	.42723	.629	-1.6316	.6075
	5a	-1.49167*	.43453	.005	-2.6304	-.3529

Table 5.50. Results of *post hoc* one way ANOVA using Tukey HSD for m1Ltrig in MIS 1, 3, 5a and 7. Mean significant difference at 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 1 and 5a.
- Pairings of MIS 1 and 3, and MIS 1 and 7 were non-significant.

Table 5.51 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of m1Ltal between MIS 1, 3, 5a and 7.

					95% Confidence Interval	
MIS	**MIS**	**Mean Difference**	**Std. Error**	**Sig.**	**Lower Bound**	**Upper Bound**
1	3	.59109*	.17041	.005	.1444	1.0378
	5a	.37659	.17364	.140	-.0786	.8317
	7	.42325	.22640	.249	-.1702	1.0167
3	1	-.59109*	.17041	.005	-1.0378	-.1444
	5a	-.21450	.20273	.716	-.7459	.3169
	7	-.16784	.24941	.907	-.8216	.4859
5a	1	-.37659	.17364	.140	-.8317	.0786
	3	.21450	.20273	.716	-.3169	.7459
	7	.04667	.25163	.998	-.6129	.7062
7	1	-.42325	.22640	.249	-1.0167	.1702
	3	.16784	.24941	.907	-.4859	.8216
	5a	-.04667	.25163	.998	-.7062	.6129

Table 5.51. Results of *post hoc* one way ANOVA using Tukey HSD for m1Ltal in MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated MIS 1 and 3 as significantly different.
- MIS 1 with both MIS 5a and 7 were non-significant.

Table 5.52 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of m1W between MIS 1, 3, 5a and 7.

					95% Confidence Interval	
MIS	**MIS**	**Mean Difference**	**Std. Error**	**Sig.**	**Lower Bound**	**Upper Bound**
1	3	.16831	.18049	.787	-.3047	.6413
	5a	-.53397*	.18716	.027	-1.0244	-.0435
	7	.66714*	.24403	.037	.0276	1.3066
3	1	-.16831	.18049	.787	-.6413	.3047
	5a	-.70228*	.21584	.009	-1.2679	-.1366
	7	.49883	.26666	.248	-.2000	1.1976

5a	1	.53397*	.18716	.027	.0435	1.0244
	3	.70228*	.21584	.009	.1366	1.2679
	7	1.20111*	.27122	.000	.4904	1.9119
7	1	-.66714*	.24403	.037	-1.3066	-.0276
	3	-.49883	.26666	.248	-1.1976	.2000
	5a	-1.20111*	.27122	.000	-1.9119	-.4904

Table 5.52. Results of *post hoc* one way ANOVA using Tukey HSD for m1W between MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 1 and 5a, and MIS 1 and 7.
- MIS 1 and 3 were found to be non-significant.

Table 5.53 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of m2L between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	.54961	.21487	.059	-.0139	1.1131
	5a	.55784	.21487	.053	-.0057	1.1213
	7	1.10667*	.26301	.000	.4169	1.7964
3	1	-.54961	.21487	.059	-1.1131	.0139
	5a	.00824	.25638	1.000	-.6641	.6806
	7	.55706	.29789	.249	-.2242	1.3383
5a	1	-.55784	.21487	.053	-1.1213	.0057
	3	-.00824	.25638	1.000	-.6806	.6641
	7	.54882	.29789	.261	-.2324	1.3300
7	1	-1.10667*	.26301	.000	-1.7964	-.4169
	3	-.55706	.29789	.249	-1.3383	.2242
	5a	-.54882	.29789	.261	-1.3300	.2324

Table 5.53. Results of *post hoc* one way ANOVA using Tukey HSD for m2L in MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 1 and 7.
- MIS 1 with both MIS 3 and 5a were non-significant.

Table 5.54 shows the results of *post hoc* one way ANOVA using Dunnett's T3 (as variances were found to be unequal by Levene's test in Table 5.47) for multiple comparisons of m2W between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	.48720*	.14482	.015	.0738	.9006
	5a	.25783	.19067	.690	-.2964	.8120
	7	.85795	.29445	.079	-.0840	1.7999
3	1	-.48720*	.14482	.015	-.9006	-.0738
	5a	-.22937	.21990	.874	-.8502	.3915
	7	.37075	.31417	.797	-.5930	1.3345
5a	1	-.25783	.19067	.690	-.8120	.2964

	3	.22937	.21990	.874	-.3915	.8502
	7	.60012	.33776	.417	-.4037	1.6039
7	1	-.85795	.29445	.079	-1.7999	.0840
	3	-.37075	.31417	.797	-1.3345	.5930
	5a	-.60012	.33776	.417	-1.6039	.4037

Table 5.54. Results of *post hoc* one way ANOVA using Dunnett's T3 for m2W in MIS 1, 3, 5a and 7. Significant result indicated by $p<0.05$.

- Dunnett's T3 indicated significant differences between MIS 1 and 3, and MIS 1 and 7.
- MIS 1 and MIS 5a were non-significant.

Table 5.55 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of DentaryL between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1.0	3.0	12.5930	6.0354	.173	-3.508	28.694
	4.6	9.5930	6.0354	.395	-6.508	25.694
	7.0	15.0930	6.0354	.073	-1.008	31.194
3.0	1.0	-12.5930	6.0354	.173	-28.694	3.508
	4.6	-3.0000	8.3435	.984	-25.258	19.258
	7.0	2.5000	8.3435	.991	-19.758	24.758
4.6	1.0	-9.5930	6.0354	.395	-25.694	6.508
	3.0	3.0000	8.3435	.984	-19.258	25.258
	7.0	5.5000	8.3435	.912	-16.758	27.758
7.0	1.0	-15.0930	6.0354	.073	-31.194	1.008
	3.0	-2.5000	8.3435	.991	-24.758	19.758
	4.6	-5.5000	8.3435	.912	-27.758	16.758

Table 5.55. Results of *post hoc* one way ANOVA using Tukey HSD for DentaryL in MIS 1, 3, 5a and 7. Significant result indicated by $p<0.05$.

- Tukey HSD did not replicate the significant result in pairwise comparisons. All comparisons were non-significant.

Table 5.56 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of p3p4D between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	.73607	.63283	.652	-.9289	2.4010
	5a	.80624	.58153	.512	-.7237	2.3362
	7	2.73190*	.84377	.010	.5120	4.9518
3	1	-.73607	.63283	.652	-2.4010	.9289
	5a	.07017	.74877	1.000	-1.8998	2.0401
	7	1.99583	.96666	.175	-.5474	4.5391
5a	1	-.80624	.58153	.512	-2.3362	.7237
	3	-.07017	.74877	1.000	-2.0401	1.8998
	7	1.92567	.93388	.176	-.5313	4.3827
7	1	-2.73190*	.84377	.010	-4.9518	-.5120
	3	-1.99583	.96666	.175	-4.5391	.5474

	5a	-1.92567	.93388	.176	-4.3827	.5313

Table 5.56. Results of *post hoc* one way ANOVA using Tukey HSD for p3p4D in MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated MIS 1 and 7 as significantly different.
- MIS 1 with both MIS 3 and 5a were non-significant.

Table 5.57 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of p3p4B between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	.66452	.38496	.318	-.3494	1.6784
	5a	-.36048	.38496	.785	-1.3744	.6534
	7	1.78286*	.51328	.005	.4310	3.1347
3	1	-.66452	.38496	.318	-1.6784	.3494
	5a	-1.02500	.48013	.153	-2.2895	.2395
	7	1.11833	.58804	.237	-.4304	2.6671
5a	1	.36048	.38496	.785	-.6534	1.3744
	3	1.02500	.48013	.153	-.2395	2.2895
	7	2.14333*	.58804	.003	.5946	3.6921
7	1	-1.78286*	.51328	.005	-3.1347	-.4310
	3	-1.11833	.58804	.237	-2.6671	.4304
	5a	-2.14333*	.58804	.003	-3.6921	-.5946

Table 5.57. Results of *post hoc* one way ANOVA using Tukey HSD for p3p4B in MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated MIS 1 and 7 to be significant.
- MIS 1 with both MIS 3 and 5a were non-significant.

Table 5.58 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of m1m2D between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	3.26183*	.85683	.002	1.0076	5.5161
	5a	2.23071*	.67055	.007	.4665	3.9949
	7	4.74071*	.95232	.000	2.2352	7.2462
3	1	-3.26183*	.85683	.002	-5.5161	-1.0076
	5a	-1.03111	.96161	.707	-3.5610	1.4988
	7	1.47889	1.17556	.592	-1.6139	4.5717
5a	1	-2.23071*	.67055	.007	-3.9949	-.4665
	3	1.03111	.96161	.707	-1.4988	3.5610
	7	2.51000	1.04758	.087	-.2461	5.2661
7	1	-4.74071*	.95232	.000	-7.2462	-2.2352
	3	-1.47889	1.17556	.592	-4.5717	1.6139
	5a	-2.51000	1.04758	.087	-5.2661	.2461

Table 5.58. Results of *post hoc* one way ANOVA using Tukey HSD for m1m2D in MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated MIS 1 and all the Pleistocene age groups as being significantly different.

Table 5.59 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of m1m2B between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	.18722	.42835	.972	-.9405	1.3150
	5a	-.76024	.35989	.159	-1.7077	.1873
	7	1.38958*	.44986	.015	.2052	2.5740
3	1	-.18722	.42835	.972	-1.3150	.9405
	5a	-.94746	.49824	.237	-2.2592	.3643
	7	1.20236	.56666	.156	-.2895	2.6942
5a	1	.76024	.35989	.159	-.1873	1.7077
	3	.94746	.49824	.237	-.3643	2.2592
	7	2.14982*	.51685	.001	.7891	3.5106
7	1	-1.38958*	.44986	.015	-2.5740	-.2052
	3	-1.20236	.56666	.156	-2.6942	.2895
	5a	-2.14982*	.51685	.001	-3.5106	-.7891

Table 5.59. Results of *post hoc* one way ANOVA using Tukey HSD for m1m2B in MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated MIS 1 and 7 as significantly different.
- MIS 1 with both MIS 3 and 5a were non-significant.

Table 5.60 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of P4W between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	1.03024	.48513	.158	-.2543	2.3148
	5a	1.10024*	.39113	.033	.0646	2.1359
	7	.16024	.80450	.997	-1.9700	2.2905
3	1	-1.03024	.48513	.158	-2.3148	.2543
	5a	.07000	.57402	.999	-1.4499	1.5899
	7	-.87000	.90760	.773	-3.2732	1.5332
5a	1	-1.10024*	.39113	.033	-2.1359	-.0646
	3	-.07000	.57402	.999	-1.5899	1.4499
	7	-.94000	.86102	.696	-3.2199	1.3399
7	1	-.16024	.80450	.997	-2.2905	1.9700
	3	.87000	.90760	.773	-1.5332	3.2732
	5a	.94000	.86102	.696	-1.3399	3.2199

Table 5.60. Results of *post hoc* one way ANOVA using Tukey HSD for P4W in MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated MIS 1 and 5a as significantly different.
- MIS 1 with MIS 3 and 7 were non-significant.

Table 5.61 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of M1L between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	1.29483*	.28635	.000	.5431	2.0466
	5a	1.02402*	.25398	.001	.3572	1.6908
	7	1.43416*	.34835	.001	.5196	2.3487
3	1	-1.29483*	.28635	.000	-2.0466	-.5431
	5a	-.27081	.32929	.844	-1.1353	.5937
	7	.13933	.40654	.986	-.9280	1.2066
5a	1	-1.02402*	.25398	.001	-1.6908	-.3572
	3	.27081	.32929	.844	-.5937	1.1353
	7	.41014	.38443	.711	-.5991	1.4194
7	1	-1.43416*	.34835	.001	-2.3487	-.5196
	3	-.13933	.40654	.986	-1.2066	.9280
	5a	-.41014	.38443	.711	-1.4194	.5991

Table 5.61. Results of *post hoc* one way ANOVA using Tukey HSD for M1L in MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated MIS 1 and all the Pleistocene age groups as significant.

Table 5.62 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of M1W between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	.64452	.41842	.419	-.4552	1.7443
	5a	1.87300*	.36717	.000	.9079	2.8381
	7	1.69035*	.55852	.018	.2223	3.1584
3	1	-.64452	.41842	.419	-1.7443	.4552
	5a	1.22848	.48321	.062	-.0416	2.4985
	7	1.04583	.64080	.367	-.6384	2.7301
5a	1	-1.87300*	.36717	.000	-2.8381	-.9079
	3	-1.22848	.48321	.062	-2.4985	.0416
	7	-.18265	.60858	.991	-1.7822	1.4169
7	1	-1.69035*	.55852	.018	-3.1584	-.2223
	3	-1.04583	.64080	.367	-2.7301	.6384
	5a	.18265	.60858	.991	-1.4169	1.7822

Table 5.62. Results of *post hoc* one way ANOVA using Tukey HSD for M1W in MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated MIS 1 and 5a, and MIS 1 and 7 as significantly different.
- MIS 1 and 3 were non-significant.

Table 5.63 shows the results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons of M2W between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	.66881	.38630	.317	-.3541	1.6917

	5a	.90937*	.27117	.008	.1913	1.6274
	7	1.09181*	.34925	.014	.1670	2.0166
3	1	-.66881	.38630	.317	-1.6917	.3541
	5a	.24056	.44363	.948	-.9341	1.4152
	7	.42300	.49523	.828	-.8883	1.7343
5a	1	-.90937*	.27117	.008	-1.6274	-.1913
	3	-.24056	.44363	.948	-1.4152	.9341
	7	.18244	.41177	.971	-.9079	1.2728
7	1	-1.09181*	.34925	.014	-2.0166	-.1670
	3	-.42300	.49523	.828	-1.7343	.8883
	5a	-.18244	.41177	.971	-1.2728	.9079

Table 5.63. Results of *post hoc* one way ANOVA using Tukey HSD for M2W in MIS 1, 3, 5a and 7. Mean difference is significant at the 0.05 level. Significant result indicated by $p<0.05$.

- Tukey HSD indicated significant differences between MIS 1 and 5a, and MIS 1 and 7.
- MIS 1 and MIS 3 were non-significant.

Table 5.64 shows the results of *post hoc* one way ANOVA using Dunnett's T3 (as M1M2L was found to have unequal variances by Levene's test (Table 5.47) for multiple comparisons of M1M2L between MIS 1, 3, 5a and 7.

MIS	MIS	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	3	2.27386	1.18777	.431	-2.8069	7.3547
	5a	1.11786	.51451	.245	-.4943	2.7300
	7	2.21686	.67823	.145	-1.0460	5.4797
3	1	-2.27386	1.18777	.431	-7.3547	2.8069
	5a	-1.15600	1.27311	.913	-5.9971	3.6851
	7	-.05700	1.34762	1.000	-4.9680	4.8540
5a	1	-1.11786	.51451	.245	-2.7300	.4943
	3	1.15600	1.27311	.913	-3.6851	5.9971
	7	1.09900	.81854	.702	-1.8168	4.0148
7	1	-2.21686	.67823	.145	-5.4797	1.0460
	3	.05700	1.34762	1.000	-4.8540	4.9680
	5a	-1.09900	.81854	.702	-4.0148	1.8168

Table 5.64. Results of *post hoc* one way ANOVA using Dunnett's T3 for M1M2L in MIS 1, 3, 5a and 7. Significant result indicated by $p<0.05$.

- Dunnett's T3 revealed no significance between the age groups.

Summary

More differences were found between measurements including modern (MIS 1) *C. lupus* than without. p4L was significant between MIS 1 and 5a, and was suggestively significant with MIS 3. p4W was significant between MIS 1 and 5a only, as were m1Ltrig and P4W. Only m1Ltal was significant between MIS 1 and 3 alone. m1W was significant between MIS 1 and both MIS 5a and 7, as were M1W and M2W. m2L was significant between MIS 1 and

7 only, as were p3p4D, p3p4B and m1m2B. m2W was significant between MIS 1 and both MIS 3 and 7, as was M1M2L. Only m1m2D and M1L were both found to be significant between MIS 1 and all the Pleistocene age groups. However, it is important to note that sample sizes for MIS 7 were small, which although Levene's tests indicated the majority of measurements had homogeneous variance, risk of errors in using small sample sizes are increased.

5.3.2.2. Temporal analysis: Pleistocene *C. lupus* from mainland Europe

As explained, due to a lack of chronological control on many of the European Pleistocene sites containing *C. lupus*, these were grouped into broad age categories as follows: 3: late Middle Pleistocene, 2.8: early Late Pleistocene, 2.4: mid Late Pleistocene, 2: late Late Pleistocene. Table 5.65 shows the results of one way ANOVA between the broad European age groups.

Measure	Age	n	mean	SD	Levene's test	one-way ANOVA
m1Ltrig	2*				$F_{(2, 12)} = 0.281$, $p=0.760$	$F_{(2,12)} = 3.637$, $p=0.058$
	2.4	4	20.41	0.813		
	2.8	8	20.07	0.894		
	3	3	18.78	0.566		
	Total	15	19.90	0.971		
m1Ltal	2*				$F_{(2, 12)} = 0.655$, $p=0.537$	$F_{(2,12)} = 0.202$, $p=0.820$
	2.4	4	7.17	0.525		
	2.8	8	7.39	0.620		
	3	3	7.27	0.522		
	Total	15	7.31	0.548		
m1W	2*				$F_{(2, 12)} = 0.223$, $p=0.803$	$F_{(2,12)} = 1.908$, $p=0.191$
	2.4	4	11.60	0.542		
	2.8	8	11.34	0.646		
	3	3	10.65	0.806		
	Total	15	11.27	0.693		

Table 5.65. Results from Levene's tests and one-way ANOVA for temporal analysis of age groups 2, 2.4, 2.8 and 3 (late Middle to late Late Pleistocene) of *C. lupus* from European sites. Results include number, mean and standard deviation for each age group, result from Levene's test of equal variances, and result of one-way ANOVA for each measurement. *indicates no individuals present in age group, hence not analysed. N/A indicates too few individuals for analysis. Significant result indicated by $p<0.05$.

- Due to low numbers of individuals, only the measurements shown were able to be analysed using ANOVA. Nonetheless, sample sizes remain small.
- Levene's test found m1Ltrig, m1Ltal and m1W as non-significant, indicating equal variances.

- One-way ANOVA indicated these measurements as non-significant, indicating no temporal differences present. Further *post hoc* tests were not carried out due to this non-significance.

5.3.2.2.1. Temporal analysis: Pleistocene *C. lupus* from mainland Europe with the modern Swedish wolf group

The European age groups containing *C. lupus* were also analysed with the modern Swedish wolf subset. Table 5.66 shows the results of Levene's test and one-way ANOVA between the age groups, with modern *C. lupus* as age group 1. Some age groups contain a low number of individuals and could not be analysed by one-way ANOVA.

Raw measure	Age	n	Mean	SD	Levene's test	one-way ANOVA
p4L	1	42	15.58	0.688	$F_{(2, 50)} = 0.065$, $p=0.937$	$F_{(2, 50)} = 3.787$, $p=0.029$
	2.4	5	16.37	0.616		
	2.8	6	16.11	0.933		
	3	N/A				
	Total	53	15.72	0.748		
p4W	1	42	8.10	0.563	$F_{(2, 49)} = 2.564$, $p=0.087$	$F_{(2, 49)} = 1.527$, $p=0.227$
	2.4	4	7.82	0.508		
	2.8	6	7.74	0.128		
	3	N/A				
	Total	52	8.03	0.537		
m1Ltrig	1	42	20.49	0.928	$F_{(3, 53)} = 0.445$, $p=0.722$	$F_{(3, 53)} = 3.553$, $p=0.020$
	2.4	4	20.41	0.813		
	2.8	8	20.07	0.894		
	3	3	18.78	0.566		
	Total	57	20.33	0.967		
m1Ltal	1	42	7.93	0.570	$F_{(3, 53)} = 0.273$, $p=0.845$	$F_{(3, 53)} = 4.484$, $p=0.007$
	2.4	4	7.17	0.525		
	2.8	8	7.39	0.620		
	3	3	7.27	0.522		
	Total	57	7.77	0.624		
m1W	1	42	11.84	0.625	$F_{(3, 53)} = 0.135$, $p=0.939$	$F_{(3, 53)} = 4.378$, $p=0.008$
	2.4	4	11.60	0.542		
	2.8	8	11.34	0.646		
	3	3	10.65	0.806		
	Total	57	11.69	0.091		
p1p4L	1	41	50.28	2.391	$F_{(2, 46)} = 0.942$, $p=0.397$	$F_{(2, 46)} = 0.730$, $p=0.488$
	2.4	4	50.63	2.354		
	2.8	4	51.88	4.203		
	3	N/A				
	Total	49	50.44	2.532		
p2p4L	1	42	43.40	1.758	$F_{(2, 48)} = 0.555$, $p=0.578$	$F_{(2, 48)} = 1.566$, $p=0.219$
	2.4	4	44.22	2.296		
	2.8	5	44.88	2.903		
	3	N/A				

	Total	51	43.61	1.938		
p3p4D	1	42	28.56	2.105	$F_{(2, 47)} = 3.324$, $p=0.045$	$F_{(2, 47)} = 2.766$, $p=0.073$
	2.4	6	26.40	1.392		
	2.8	2	28.85	4.702		
	3	N/A				
	Total	50	28.31	2.207		
p3p4B	1	42	13.11	1.133	$F_{(2, 43)} = 2.562$, $p=0.089$	$F_{(2, 43)} = 0.085$, $p=0.918$
	2.4	2	12.80	0.212		
	2.8	2	13.25	2.319		
	3	N/A				
	Total	46	13.11	1.138		
M1M2L	1	43	24.07	1.085	$F_{(2, 44)} = 0.613$, $p=0.546$	$F_{(2, 44)} = 3.527$, $p=0.038$
	2.4	2	21.95	1.895		
	2.8	2	23.63	1.457		
	3	N/A				
	Total	47	23.96	1.179		

Table 5.66. Results from Levene's test and one-way ANOVA for age groups 1, 2.4, 2.8 and 3 for *C. lupus* from Europe. Results include number, mean and standard deviation for each age group, result from Levene's test of equal variances, and result of one-way ANOVA for each measurement. N/A indicates too few individuals for analysis. Significance indicated by $p<0.05$.

- Levene's test found p3p4D as significant, indicating unequal variances. As previous, as measurement is both normally distributed and independent, the ANOVA result will be kept.
- Remaining measurements were non-significant, thus equal in variance.
- One-way ANOVA found p4L, m1Ltrig, m1Ltal, m1W and M1M2L as significant, indicating temporal differences between the age groups.

The significant measurements will be further analysed by *post hoc* tests using Tukey HSD for multiple comparisons between age groups. Table 5.67 shows the results for p4L between modern *C. lupus* (group 1) and age groups 2.4, 2.8 focussing on differences with the modern group (1).

Age group	Age group	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1.0	2.4	-.79033	.33621	.058	-1.6024	.0217
	2.8	-.52500	.31016	.218	-1.2742	.2242
2.4	1.0	.79033	.33621	.058	-.0217	1.6024
	2.8	.26533	.43033	.812	-.7741	1.3048
2.8	1.0	.52500	.31016	.218	-.2242	1.2742
	2.4	-.26533	.43033	.812	-1.3048	.7741

Table 5.67. Results of *post hoc* one way ANOVA using Tukey HSD for p4L in age groups 1, 2.4 and 2.8. Mean difference is significant at the 0.05 level. Significance indicated by $p<0.05$.

- Tukey HSD did not replicate the significant result in pairwise comparisons. All comparisons were non-significant.

Table 5.68 shows the results for m1Ltrig between age groups 1 and 2.4, 2.8, 3, focussing on differences with the modern age group (1).

Age group	Age group	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1.0	2.4	.08024	.47443	.998	-1.1782	1.3386
	2.8	.41774	.34975	.633	-.5100	1.3454
	3.0	1.70190*	.54183	.014	.2647	3.1391
2.4	1.0	-.08024	.47443	.998	-1.3386	1.1782
	2.8	.33750	.55521	.929	-1.1352	1.8102
	3.0	1.62167	.69247	.101	-.2151	3.4584
2.8	1.0	-.41774	.34975	.633	-1.3454	.5100
	2.4	-.33750	.55521	.929	-1.8102	1.1352
	3.0	1.28417	.61381	.169	-.3439	2.9123
3.0	1.0	-1.70190*	.54183	.014	-3.1391	-.2647
	2.4	-1.62167	.69247	.101	-3.4584	.2151
	2.8	-1.28417	.61381	.169	-2.9123	.3439

Table 5.68. Results of *post hoc* one way ANOVA using Tukey HSD for m1Ltrig in age groups 1 and 2.4, 2.8 and 3. Mean difference is significant at the 0.05 level. Significance indicated by $p<0.05$.

- Tukey HSD indicated significant differences between modern group 1 and age group 3.
- Group 1 with both age groups 2.4 and 2.8 were non-significant.

Table 5.69 shows the results for m1Ltal between age groups 1 and 2.4, 2.8, 3, focussing on differences with the modern age group (1).

Age group	Age group	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1.0	2.4	.75964	.29978	.066	-.0355	1.5548
	2.8	.53839	.22100	.083	-.0478	1.1246
	3.0	.66214	.34237	.226	-.2460	1.5703
2.4	1.0	-.75964	.29978	.066	-1.5548	.0355
	2.8	-.22125	.35082	.922	-1.1518	.7093
	3.0	-.09750	.43755	.996	-1.2581	1.0631
2.8	1.0	-.53839	.22100	.083	-1.1246	.0478
	2.4	.22125	.35082	.922	-.7093	1.1518
	3.0	.12375	.38785	.989	-.9050	1.1525
3.0	1.0	-.66214	.34237	.226	-1.5703	.2460
	2.4	.09750	.43755	.996	-1.0631	1.2581
	2.8	-.12375	.38785	.989	-1.1525	.9050

Table 5.69. Results of *post hoc* one way ANOVA using Tukey HSD for m1Ltal in group 1 and age groups 2.4, 2.8 and 3. Mean difference is significant at the 0.05 level Significance indicated by $p<0.05$.

- Tukey HSD did not replicate this significance, with all comparisons non-significant.

Table 5.70 shows the results for m1W between age groups 1, 2.4, 2.8 and 3, focussing on differences with the modern group 1.

Age group	Age group	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1.0	2.4	.24131	.33014	.884	-.6344	1.1170
	2.8	.50381	.24338	.176	-.1417	1.1494
	3.0	1.19048*	.37704	.014	.1904	2.1906
2.4	1.0	-.24131	.33014	.884	-1.1170	.6344
	2.8	.26250	.38635	.904	-.7623	1.2873
	3.0	.94917	.48187	.212	-.3290	2.2273
2.8	1.0	-.50381	.24338	.176	-1.1494	.1417
	2.4	-.26250	.38635	.904	-1.2873	.7623
	3.0	.68667	.42713	.383	-.4463	1.8196
3.0	1.0	-1.19048*	.37704	.014	-2.1906	-.1904
	2.4	-.94917	.48187	.212	-2.2273	.3290
	2.8	-.68667	.42713	.383	-1.8196	.4463

Table 5.70. Results of *post hoc* one way ANOVA using Tukey HSD for m1W in group 1 and age groups 2.4, 2.8 and 3. Mean difference is significant at the 0.05 level. Significance indicated by $p<0.05$.

- Tukey HSD indicated significant differences between group 1 and age group 3.
- Modern group 1 and both age groups 2.4 and 2.8 were non-significant.

Table 5.71 shows the results for M1M2L between MIS 1 and age groups 1, 2.4, 2.8 and 3, focussing on differences with age group 1 (modern *C. lupus*).

Age group	Age group	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1.0	2.4	2.12186*	.80961	.032	.1582	4.0856
	2.8	.44186	.80961	.849	-1.5218	2.4056
2.4	1.0	-2.12186*	.80961	.032	-4.0856	-.1582
	2.8	-1.68000	1.11923	.300	-4.3947	1.0347
2.8	1.0	-.44186	.80961	.849	-2.4056	1.5218
	2.4	1.68000	1.11923	.300	-1.0347	4.3947

Table 5.71. Results of *post hoc* one way ANOVA using Tukey HSD for M1M2L in age group 1 and 2.4 and 2.8. Mean difference is significant at the 0.05 level. Significance indicated by $p<0.05$.

- Tukey HSD indicated significant differences between age group 1 and age group 2.4.
- Modern age group 1 and 2.8 were non-significant.

As previously mentioned, due to low numbers of individuals some measurements are only present in the mid Late Pleistocene age group 2.4. *t* tests were therefore used to compare these measurements with the recent Swedish wolves. Table 5.72 shows the results.

Measure	Age	n	Mean	SD	Levene's test	*t* test
m2L	1	42	12.11	0.689	$F_{(45)} = 1.273$, $p=0.265$	$t_{45} = 1.308$, $P=0.197$
	2.4	5	11.69	0.476		
m2W	1	42	9.17	0.434	$F_{(45)} = 0.621$, $p=0.435$	$t_{45} = 0.889$, $P=0.379$
	2.4	5	8.98	0.562		
p1m3L	1	42	96.08	2.769	$F_{(44)} = 0.152$, $p=0.698$	$t_{44} = -0.699$, $P=0.488$
	2.4	4	97.09	2.447		
p2m3L	1	42	89.45	2.678	$F_{(43)} = 0.111$, $p=0.740$	$t_{43} = -0.825$, $P=0.414$
	2.4	3	90.78	3.150		
DentaryL	1	43	178.09	8.411	$F_{(43)} = 0.001$, $p=0.979$	$t_{43} = 1.409$, $P=0.166$
	2.4	2	169.50	9.192		
m1m2D	1	42	34.03	2.410	$F_{(42)} = 0.051$, $p=0.823$	$t_{42} = 2.266$, $P=0.029$
	2.4	2	30.08	2.510		
m1m2B	1	42	13.12	1.156	$F_{(42)} = 3.337$, $p=0.075$	$t_{42} = 0.052$, $P=0.958$
	2.4	2	13.08	0.064		
	2.4	2	21.95	1.895		

Table 5.72. Results from Levene's test and *t* tests age groups 1 (modern *C. lupus*) and 2.4 for *C. lupus* from mainland European sites. Significance indicated by $p<0.05$.

- Levene's test found all analysed measurements as non-significant, indicating equal variances.
- *t* tests found m1m2D as significant, indicating differences between age group 2.4 and recent *C. lupus*.

Summary

Only p4L, m1Ltrig, m1Ltal, m1W and M1M2L were found by one-way ANOVA as significant. Tukey HSD *post hoc* tests were used on these significant measurements enabling multiple comparisons. However, although found to be significant by one-way ANOVA, both p4L and m1Ltal were found to be non-significant by *post hoc* tests. *Post hoc* tests found m1Ltrig and m1W to be significant between MIS 1 and age group 3, with M1M2L significant between MIS 1 and age group 2.4. Due to the lack of individuals in some age groups, *t* tests were used to compare the modern group with age group 2.4 (as no other individuals were present in the remaining age groups), which found m1m2D to be significant.

In contrast to the temporal analysis of modern Swedish wolves against British *C. lupus* material, the measurements from European Pleistocene *C. lupus* were more similar to those of modern *C. lupus*.

As with the analyses of British Pleistocene *C. lupus*, small sample sizes were present. Although Levene's tests were used to check homogeneity of variance, risk of errors relating to sample size remained an issue here.

5.3.2.3. Temporal analysis: *C. mosbachensis* from Britain

As temporal variation in the dietary measurements was apparent in the British Pleistocene populations of *C. lupus*, it was appropriate to investigate whether similar variation was present earlier in time, in *C. mosbachensis*. However, due to low numbers of individuals, one-way ANOVA was only able to be applied to m2L and m2W, shown in Table 5.73.

For the purposes of the analysis, the coeval sites of Boxgrove and Sidestrand were combined as a single group, and then compared with the slightly older Westbury-sub-Mendip, and MIS 17 West Runton. Nonetheless, problems small sample sizes were an ongoing issue for the analysis of *C. mosbachensis* (see 5.3.2.).

The remaining measurements were analysed using *t* tests, shown in Table 5.73.

Measure	Site	n	Mean	SD	Levene's test	one-way ANOVA
m2L	BXG/SSD	2	9.98	0.339	$F_{(2,10)} = 1.035$, $p=0.390$	$F_{(2,10)} = 6.255$, $p=0.017$
	WSM	9	10.21	0.671		
	WRTN	2	8.39	0.806		
	Total	13	9.90	0.905		
m2W	BXG/SSD	2	7.24	0.233	$F_{(2,9)} = 1.664$, $p=0.243$	$F_{(2,9)} = 6.543$, $p=0.018$
	WSM	8	7.66	0.512		
	WRTN	2	6.28	0.488		
	Total	12	7.36	0.689		

Table 5.73. Results from Levene's test and one way ANOVA of early Middle Pleistocene *C. mosbachensis* from Britain. BXG/SSD: Boxgrove/Sidestrand, WSM: Westbury-sub-Mendip, WRTN: West Runton. Significance indicated by $p<0.05$.

- Levene's test indicated both measurements had equal variances ($p>0.05$).
- One-way ANOVA found both measurements to be significant, indicating temporal differences over the early Middle Pleistocene.

These significant measurements were further analysed using *post hoc* tests, with Tukey HSD for multiple comparisons. Table 5.74 shows the results for m2L between Cromerian Complex groups.

Age group	Age group	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
BXG/SSD	WSM	-.23333	.51628	.895	-1.6486	1.1819
	WRTN	1.59000	.66042	.086	-.2204	3.4004
WSM	BXG/SSD	.23333	.51628	.895	-1.1819	1.6486
	WRTN	1.82333*	.51628	.014	.4081	3.2386
WRTN	BXG/SSD	-1.59000	.66042	.086	-3.4004	.2204
	WSM	-1.82333*	.51628	.014	-3.2386	-.4081

Table 5.74. Results of *post hoc* one-way ANOVA using Tukey HSD for m2L in BXG/SSD, WSM and WRTN. Mean difference is significant at the 0.05 level. Significance indicated by $p<0.05$.

- Tukey HSD indicated significant differences related Westbury-sub-Mendip (MIS 13) and the older site of West Runton (MIS 17).

Table 5.75 shows the results of *post hoc* one-way ANOVA using Tukey HSD for multiple comparisons for m2W.

Age group	Age group	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
BXG/SSD	WSM	-.42250	.38439	.538	-1.4957	.6507
	WRTN	.96000	.48622	.174	-.3975	2.3175
WSM	BXG/SSD	.42250	.38439	.538	-.6507	1.4957
	WRTN	1.38250*	.38439	.014	.3093	2.4557
WRTN	BXG/SSD	-.96000	.48622	.174	-2.3175	.3975
	WSM	-1.38250*	.38439	.014	-2.4557	-.3093

Table 5.75. Results of *post hoc* one way ANOVA using Tukey HSD for m2W in BXG/SSD, WSM and WRTN. Significance indicated by $p<0.05$.

- Tukey HSD indicated significant differences between Westbury-sub-Mendip (MIS 13) and West Runton (MIS 17).

The remaining measurements were analysed using *t* tests between the similarly aged Boxgrove and Sidestrand, and the slightly older site of Westbury-sub-Mendip. Table 5.76 shows the results.

Measure	Age group	n	Mean	SD	Levene's test	*t* test
p4L	BXG/SSD	3	14.17	1.097	$F_{(8)} = 0.418$, $p=0.536$	$t_8 = 1.180$, $p=0.272$
	WSM	7	13.42	0.324		
p4W	BXG/SSD	3	6.38	0.6223	$F_{(8)} = 0.0001$, $p=0.996$	$t_8 = 0.637$, $p=0.542$
	WSM	7	6.11	0.598		
m1Ltrig	BXG/SSD	4	15.59	0.999	$F_{(9)} = 0.418$, $p=0.534$	$t_9 = -1.275$, $p=0.234$
	WSM	7	16.48	1.164		
m1Ltal	BXG/SSD	4	6.87	0.301	$F_{(12)} = 0.996$, $p=0.338$	$t_{12} = 0.806$, $p=0.436$
	WSM	10	6.68	0.443		
m1W	BXG/SSD	4	9.14	0.899	$F_{(9)} = 0.362$, $p=0.562$	$t_9 = -0.613$, $p=0.555$
	WSM	7	9.41	0.573		
m2L	BXG/SSD	2	9.98	0.339	$F_{(9)} = 1.767$, $p=0.217$	$t_9 = -0.465$, $p=0.653$
	WSM	9	10.21	0.671		
m2W	BXG/SSD	2	7.24	0.233	$F_{(8)} = 2.904$, $p=0.127$	$t_8 = -1.100$, $p=0.303$
	WSM	8	7.66	0.512		
p1p4L	N/A					
p2p4L	BXG/SSD	3	40.59	2.546	$F_{(4)} = 0.013$, $p=0.915$	$t_4 = 1.514$, $p=0.205$
	WSM	3	37.37	2.664		
p1m3L	N/A					
p2m3L	BXG/SSD	3	78.44	5.093	$F_{(3)} = 0.743$, $p=0.452$	$t_3 = -0.100$, $p=0.926$
	WSM	2	78.86	3.274		
DentaryL	N/A					
p3p4D	BXG/SSD	3	18.917	3.223	$F_{(4)} = 1.646$, $p=0.269$	$t_4 = -0.282$, $p=0.792$
	WSM	3	19.503	1.608		
p3p4B	BXG/SSD	3	9.10	2.050	$F_{(4)} = 5.384$,	$t_4 = -0.227$,

	WSM	3	9.39	0.751	p=0.081	p=0.831
m1m2D	N/A					
m1m2B	N/A					
P3L	BXG/SSD	4	13.42	0.848	$F_{(5)}$ = 0.452, p=0.531	t_5 = -1.385, p=0.225
	WSM	3	14.23	0.613		
P4L	BXG/SSD	6	21.79	0.885	$F_{(10)}$ = 0.896, p=0.366	t_{10} = -4.660, p=0.001
	WSM	6	23.72	0.494		
P4W	BXG/SSD	3	10.24	0.306	$F_{(6)}$ = 2.712, p=0.151	t_6 = -1.563, p=0.169
	WSM	5	11.22	1.033		
M1L	BXG/SSD	4	13.36	0.236	$F_{(13)}$ = 4.898, p=0.045	$t_{12.677}$ = -0.801, p=0.438*
	WSM	11	13.59	0.887		
M1W	BXG/SSD	3	18.17	1.246	$F_{(11)}$ = 0.002, p=0.969	t_{11} = -0.670, p=0.517
	WSM	10	18.69	1.165		
M2L	BXG/SSD	4	6.85	0.907	$F_{(9)}$ = 0.512, p=0.492	t_9 = -2.234, p=0.052
	WSM	7	8.01	0.787		
M2W	BXG/SSD	4	11.57	1.072	$F_{(9)}$ = 0.045, p=0.837	t_9 = -0.880, p=0.402
	WSM	7	12.17	1.088		
P1P4L	N/A					
P1M2L	N/A					
C1M2L	N/A					
M1M2L	N/A					

Table 5.76. Results of *t* tests for Cromerian age groups: Boxgrove and Sidestrand combined and compared to Westbury-sub-Mendip *C. mosbachensis*. *indicates *t* test result with equal variance not assumed, based on significant Levene's test (p<0.05) indicating unequal variances. Significance indicated by p<0.05.

- Levene's tests found M1L as significant, indicating unequal variance. The subsequent *t* test result for this measurement therefore assumes unequal variance.
- All other measurements were found by Levene's tests as non-significant, and hence of equal variance.

The *t* tests found P4L as significant (p<0.05) between the age differentiated sites. The remaining measurements were non-significant, indicating no temporal variation present.

Summary

As Boxgrove and Sidestrand are of similar age, these groups were combined representing a young MIS 13 group. The age difference between these sites and Westbury-sub-Mendip is well established, and thus Westbury-sub-Mendip was compared to this younger group. Only m2 measurements contained individuals from West Runton (MIS 17), and so one-way ANOVA was only possible for these measurements. One-way ANOVA was significant, and further *post hoc* tests using Tukey HSD for multiple comparisons identified the significance related to differences between Westbury-sub-Mendip and West Runton. Although variances were homogeneous, the increased risk of errors relating to small sample sizes remained present.

t tests between the combined Boxgrove/Sidestrand group and Westbury-sub-Mendip were carried out, and highlighted P4L as significant. The majority of remaining measurements were non-significant, indicating no temporal differences between these groups.

5.3.2.4. Temporal analysis: *C. mosbachensis* from Europe

The presence of temporal variation was also investigated in *C. mosbachensis* from sites on the European mainland. However, due to low numbers of individuals in the broad age groups, one-way ANOVA was not possible. Table 5.77 shows the results of *t* tests between age group 3.4 (mid Middle Pleistocene) and age group 4 (late Early Pleistocene).

Measure	Age group	n	Mean	SD	Levene's test	*t* test
m1Ltrig	3.4	3	15.56	1.690	$F_{(12)} = 4.810$, $p=0.049$	$t_{2.151} = -0.834$, $P=0.487$*
	4	11	16.39	0.624		
m1Ltal	3.4	4	6.65	0.632	$F_{(12)} = 1.513$, $p=0.242$	$t_{12} = -0.221$, $P=0.829$
	4	10	6.71	0.327		
m1W	3.4	3	8.84	0.992	$F_{(11)} = 5.267$, $p=0.042$	$t_{2.197} = -0.601$, $P=0.604$*
	4	10	9.19	0.398		
m2L	3.4	2	10.15	1.011	$F_{(12)} = 0.162$, $p=0.695$	$t_{12} = -0.441$, $P=0.667$
	4	12	10.42	0.228		
m2W	3.4	2	7.24	0.509	$F_{(11)} = 0.304$, $p=0.593$	$t_{11} = -0.906$, $P=0.384$
	4	11	8.08	1.260		
m1m2D	3.4	2	22.11	3.104	$F_{(7)} = 1.832$, $p=0.218$	$t_{7} = -0.129$, $P=0.90$
	4	7	22.31	1.736		
m1m2B	3.4	2	9.58	0.375	$F_{(7)} = 0.583$, $p=0.470$	$t_{7} = -1.201$, $P=0.269$
	4	7	10.07	0.539		

Table 5.77. Results from *t* tests of age groups 3.4 and 4 (mid Middle Pleistocene and late Early Pleistocene) *C. mosbachensis* from mainland European sites. *indicates *t* test result with equal variance not assumed, based on significant Levene's test ($p<0.05$) indicating unequal variances. Significance indicated by $p<0.05$.

- Due to low numbers of individuals, analysis of many measurements was not possible. Sample size of analysed measurements also remains low.
- Levene's test found m1Ltrig and m1W to be significant, indicating unequal variances. Subsequent *t* test result for both these measurements assumes unequal variances.
- The remaining measurements were found by Levene's test to be non-significant.
- *t* tests found m1Ltrig, m1Ltal, m1W, m2L, m2W, m1m2D, m1m2B to be non-significant, and hence having no temporal difference.

5.3.2.5. Temporal analysis: *C. mosbachensis* from Britain and Europe compared

Although temporal differences in *C. mosbachensis* from both Britain and mainland Europe were minimal (only m2L and m2W in Britain was found as significant), statistical comparisons were made between sites of the early Middle Pleistocene Cromerian Complex in Britain (combined sites of Boxgrove, Sidestrand, Westbury-sub-Mendip and West Runton) and the late Early Pleistocene in Europe (Untermassfeld). However, sample size is low for some measurements introducing potential errors into the analyses (see 5.3.2.). The results are shown in Table 5.78.

Measure	Age group	n	Mean	SD	Levene's test	*t* test
p4L	Crom	10	13.65	0.943	$F_{(20)} = 0.706$, $p=0.411$	$t_{20} = 0.108$, $P=0.915$
	UMF	12	13.61	0.576		
p4W	Crom	10	6.19	0.584	$F_{(20)} = 0.2.200$, $p=0.154$	$t_{20} = -0.343$, $P=0.735$
	UMF	12	6.27	0.382		
m1Ltrig	Crom	11	16.16	1.146	$F_{(20)} = 2.991$, $p=0.099$	$t_{20} = -0.585$, $P=0.565$
	UMF	11	16.39	0.624		
m1Ltal	Crom	14	6.73	0.407	$F_{(22)} = 0.617$, $p=0.441$	$t_{22} = 0.155$, $P=0.878$
	UMF	10	6.71	0.327		
m1W	Crom	10	9.34	0.705	$F_{(18)} = 2.750$, $p=0.115$	$t_{18} = 0.598$, $P=0.557$
	UMF	10	9.19	0.398		
m2L	Crom	13	9.90	0.905	$F_{(21)} = 0.261$, $p=0.615$	$t_{21} = -1.700$, $P=0.104$
	UMF	10	10.52	0.818		
m2W	Crom	12	7.36	0.689	$F_{(18)} = 0.956$, $p=0.341$	$t_{18} = -1.732$, $P=0.100$
	UMF	9	8.26	1.335		
p1p4L	Crom	4	42.79	1.746	$F_{(9)} = 0.000$, $p=1.000$	$t_{9} = -0.448$, $P=0.665$
	UMF	7	43.33	2.031		
p2p4L	Crom	7	39.33	2.820	$F_{(14)} = 1.597$, $p=0.227$	$t_{14} = 1.981$, $P=0.068$
	UMF	9	36.90	2.098		
p1m3L	Crom	3	82.98	3.378	$F_{(7)} = 0.219$, $p=0.654$	$t_{7} = 0.521$, $P=0.618$
	UMF	6	81.96	2.512		
p2m3L	Crom	5	78.60	3.963	$F_{(10)} = 5.029$, $p=0.049$	$t_{5.294} = 1.259$, $P=0.187$*
	UMF	7	76.20	1.877		
DentaryL	N/A					
p3p4D	Crom	7	19.34	2.127	$F_{(14)} = 0.024$, $p=0.879$	$t_{14} = 0.204$, $P=0.841$
	UMF	9	19.13	1.844		
p3p4B	Crom	7	9.20	1.275	$F_{(14)} = 1.192$, $p=0.293$	$t_{14} = 0.389$, $P=0.703$
	UMF	9	9.00	0.764		
m1m2D	Crom	5	21.31	2.374	$F_{(10)} = 0.419$, $p=0.532$	$t_{10} = -0.849$, $P=0.416$
	UMF	7	22.31	1.736		
m1m2B	Crom	5	9.74	1.023	$F_{(10)} = 2.553$, $p=0.141$	$t_{10} = -0.733$, $P=0.481$
	UMF	7	10.07	0.539		
P3L	Crom	7	13.77	0.819	$F_{(9)} = 0.000$, $p=0.987$	$t_{9} = 1.184$, $P=0.267$
	UMF	4	13.17	0.791		
P4L	Crom	11	22.62	1.197	$F_{(13)} = 0.051$, $p=0.825$	$t_{13} = 0.484$, $P=0.636$
	UMF	4	22.28	1.307		
P4W	Crom	9	10.87	0.887	$F_{(11)} = 0.528$, $p=0.483$	$t_{11} = -0.553$, $P=0.592$
	UMF	4	11.15	0.699		
M1L	Crom	16	13.47	0.772	$F_{(18)} = 2.471$, $p=0.133$	$t_{18} = -0.627$, $P=0.538$
	UMF	4	13.72	0.334		

M1W	Crom	14	18.45	1.198	$F_{(15)} = 0.209$, $p=0.654$	$t_{15} = -1.062$, $P=0.305$
	UMF	3	19.25	1.109		
M2L	Crom	11	7.59	0.980	$F_{(13)} = 0.624$, $p=0.444$	$t_{13} = -0.185$, $P=0.856$
	UMF	4	7.69	0.679		
M2W	Crom	11	11.95	1.070	$F_{(13)} = 0.021$, $p=0.886$	$t_{13} = -1.060$, $P=0.309$
	UMF	4	12.62	1.140		
P1P4L	Crom	2	57.64	3.217	$F_{(2)} = 0.000$, $p=1.000$	$t_{2} = -0.218$, $P=0.848$
	UMF	2	58.34	3.217		
P1M2L	N/A					
C1M2L	N/A					
M1M2L	Crom	5	19.40	1.387	$F_{(6)} = 0.869$, $p=0.387$	$t_{6} = -1.061$, $P=0.330$
	UMF	3	20.36	0.885		

Table 5.78. Results from *t* test of grouped British early Middle Pleistocene (Crom) sites (Boxgrove, Sidestrand, Westbury-sub-Mendip, Overstrand (p2p4L, p3p4D, p3p4B) and West Runton) with (late Early Pleistocene) Untermassfeld (UMF). *indicates *t* test result with equal variance not assumed, based on significant Levene's test ($p<0.05$) indicating unequal variances. N/A indicates too few individuals for analysis. Significance indicated by $p<0.05$.

- Levene's test found p2m3L to be significant, indicating unequal variance. The subsequent *t* test does not assume equality.
- Levene's test found the remaining measurements to be non-significant.
- *t* tests found all analysed measurements to be non-significant, indicating no temporal differences.
- A lack of regional differences can also be inferred from these results, which will be discussed in Chapter 6.

5.3.2.6. Temporal analysis: *C. etruscus* from Europe

The presence of temporal variation was also explored in *C. etruscus*. However, as data were only present from Olivola (Olivola F.U.) and the Upper Valdarno (Tasso F.U.), *t* tests were used to compare the differences in age. Small sample sizes are also present for some measurements, increasing the risk of errors into the analysis (see 5.3.2.). Table 5.79 shows the results.

Measure	Age group	n	Mean	SD	Levene's test	t test
p4L	UV	12	15.07	0.625	$F_{(14)} = 0.603$, $p=0.450$	$t_{14} = -0.512$, $P=0.616$
	OLV	4	15.27	0.806		
p4W	UV	11	6.98	0.397	$F_{(13)} = 1.091$, $p=0.315$	$t_{13} = 1.841$, $P=0.089$
	OLV	4	6.59	0.264		
m1Ltrig	UV	10	16.88	0.993	$F_{(12)} = 0.020$, $p=0.890$	$t_{12} = -0.314$, $P=0.759$
	OLV	4	17.07	0.999		
m1Ltal	UV	11	6.90	0.369	$F_{(13)} = 4.130$, $p=0.063$	$t_{13} = 0.139$, $P=0.891$
	OLV	4	6.87	0.032		
m1W	UV	11	9.67	0.436	$F_{(13)} = 2.296$, $p=0.154$	$t_{13} = 0.420$, $P=0.681$
	OLV	4	9.57	0.246		

m2L	UV	10	11.17	0.690	$F_{(13)} = 0.049$, $p=0.828$	$t_{13} = 1.023$, $P=0.325$
	OLV	5	10.77	0.807		
m2W	UV	8	7.96	0.410	$F_{(10)} = 0.066$, $p=0.803$	$t_{10} = 0.946$, $P=0.366$
	OLV	4	7.71	0.479		
p1p4L	UV	7	48.30	2.658	$F_{(9)} = 0.547$, $p=0.478$	$t_{9} = 0.004$, $P=0.997$
	OLV	4	48.30	2.052		
p2p4L	UV	7	41.32	2.231	$F_{(10)} = 0.051$, $p=0.826$	$t_{10} = 0.185$, $P=0.857$
	OLV	5	41.09	2.029		
p1m3L	UV	4	88.66	6.051	$F_{(6)} = 3.753$, $p=0.101$	$t_{6} = -0.009$, $P=0.993$
	OLV	4	88.69	1.602		
p2m3L	UV	4	81.24	4.839	$F_{(7)} = 0.397$, $p=0.549$	$t_{7} = -0.763$, $P=0.471$
	OLV	5	83.35	3.466		
DentaryL	N/A					
p3p4D	UV	8	21.27	3.013	$F_{(11)} = 3.840$, $p=0.076$	$t_{11} = -0.157$, $P=0.878$
	OLV	5	21.49	1.369		
p3p4B	UV	8	10.12	1.032	$F_{(11)} = 0.004$, $p=0.950$	$t_{11} = 1.076$, $P=0.305$
	OLV	5	9.50	0.963		
m1m2D	UV	9	23.86	0.738	$F_{(12)} = 0.324$, $p=0.580$	$t_{12} = -1.656$, $P=0.124$
	OLV	5	25.84	2.011		
m1m2B	UV	7	10.57	0.250	$F_{(9)} = 2.646$, $p=0.138$	$t_{9} = -0.513$, $P=0.620$
	OLV	4	10.68	0.457		
P3L	UV	3	14.29	0.035	$F_{(3)} = 297.037$, $p=0.0001$	$t_{1.026} = 0.483$, $P=0.712$*
	OLV	2	14.21	0.247		
P4L	UV	3	23.04	1.367	$F_{(5)} = 0.049$, $p=0.834$	$t_{5} = 0.898$, $P=0.410$
	OLV	4	22.173	1.183		
P4W	UV	3	12.16	0.803	$F_{(5)} = 0.215$, $p=0.662$	$t_{5} = 2.048$, $P=0.096$
	OLV	4	11.09	0.602		
M1L	UV	4	15.56	0.285	$F_{(7)} = 7.149$, $p=0.032$	$t_{4.982} = -0.019$, $P=0.986$*
	OLV	5	15.57	0.889		
M1W	UV	4	20.22	0.455	$F_{(7)} = 4.170$, $p=0.080$	$t_{7} = -0.282$, $P=0.786$
	OLV	5	20.42	1.328		
M2L	UV	2	7.89	0.1556	$F_{(4)} = 0.881$, $p=0.401$	$t_{4} = 0.564$, $P=0.603$
	OLV	4	7.71	0.410		

Table 5.79. Results from *t* tests of Olivola and the Upper Valdarno of *C. etruscus* from Italy. *indicates *t* test result with equal variance not assumed, based on significant Levene's test ($p<0.05$) indicating unequal variances. N/A indicates too few individuals for analysis. Significance indicated by $p<0.05$.

- Due to low numbers of individuals, it was not possible to analyse all measurements for these age groups.
- Levene's test found P3L and M1L to be significant, indicating unequal variances. The subsequent *t* test result for these measurements assumes unequal variance.
- Levene's test the remaining measurements to be non-significant.
- *t* tests found all measurements to be non-significant, indicating no temporal variation in *C. etruscus* between the Olivola and Tasso F.U.s.

Unfortunately, due to only having data from *C. arnensis* from the Upper Valdarno Basin, it was not possible to examine temporal variation.

5.3.3. Regional analysis of Pleistocene *C. lupus* from Britain and Europe

Although more temporal differences were found in the measurements in Britain than in the mainland European sites, it is of interest to examine how both regions compare to each other over the same time periods.

The British dataset is best represented by MIS 3, 5a and 7, based on the high number of individuals present in each grouping. For the mainland European sites, the highest number of individuals in broad European age group terms is in groups 2.4 (mid Late Pleistocene, MIS 3 equivalent) and 2.8 (early Late Pleistocene, MIS 5e-a equivalent), although fewer individuals in these grouping meant that some measurements could not be compared. Nonetheless, small sample size issues remain present in the analysis (see 5.3.2.). Table 5.80 shows the results from *t* tests between MIS 3 and age group 2.4.

Measure	Age group	n	Mean	SD	Levene's test	*t* test
p4L	3	17	16.14	0.674	$F_{(20)} = 0.006$, $p=0.939$	$t_{20} = -0.677$, $p=0.506$
	2.4	5	16.37	0.616		
p4W	3	17	8.22	0.474	$F_{(19)} = 0.049$, $p=0.827$	$t_{19} = 1.498$, $p=0.151$
	2.4	4	7.818	0.508		
m1Ltrig	3	23	20.41	1.300	$F_{(25)} = 1.160$, $p=0.292$	$t_{25} = 0.011$, $p=0.992$
	2.4	4	20.41	0.813		
m1Ltal	3	22	7.33	0.529	$F_{(24)} = 0.096$, $p=0.760$	$t_{24} = 0.553$, $p=0.585$
	2.4	4	7.17	0.525		
m1W	3	23	11.54	0.740	$F_{(25)} = 0.189$, $p=0.667$	$t_{25} = -0.155$, $p=0.878$
	2.4	4	11.60	0.542		
m2L	3	17	11.56	0.574	$F_{(20)} = 0.431$, $p=0.519$	$t_{20} = -0.470$, $p=0.643$
	2.4	5	11.69	0.213		
m2W	3	16	8.68	0.514	$F_{(19)} = 0.164$, $p=0.690$	$t_{19} = -1.114$, $p=0.279$
	2.4	5	8.98	0.562		
p1p4L	3	11	50.74	3.227	$F_{(13)} = 1.372$, $p=0.262$	$t_{13} = 0.064$, $p=0.950$
	2.4	4	50.63	2.355		
p2p4L	3	12	44.86	2.917	$F_{(14)} = 0.627$, $p=0.442$	$t_{14} = 0.396$, $p=0.698$
	2.4	4	44.22	2.30		
p1m3L	3	7	96.59	3.953	$F_{(9)} = 1.143$, $p=0.313$	$t_{9} = -0.224$, $p=0.828$
	2.4	4	97.09	2.447		
p2m3L	3	8	90.18	4.087	$F_{(9)} = 0.479$, $p=0.506$	$t_{9} = -0.230$, $p=0.824$
	2.4	3	90.78	3.150		
DentaryL	3	2	165.5	6.364	N/A	$t_{2} = -0.506$, $p=0.663$
	2.4	2	169.5	9.192		
p3p4D	3	12	27.82	1.350	$F_{(16)} = 0.066$, $p=0.801$	$t_{16} = 2.092$, $p=0.053$
	2.4	6	26.40	1.392		
p3p4B	3	12	12.45	0.864	$F_{(12)} = 2.393$, $p=0.148$	$t_{12} = -0.555$, $p=0.589$
	2.4	2	12.80	0.212		
m1m2D	3	9	30.77	2.499	$F_{(9)} = 0.003$, $p=0.955$	$t_{9} = 0.355$, $p=0.731$
	2.4	2	30.08	2.510		
m1m2B	3	9	12.93	1.568	$F_{(9)} = 3.014$, $p=0.117$	$t_{9} = -0.125$, $p=0.904$
	2.4	2	13.08	0.064		
P3L	N/A					
P4L	N/A					

P4W	N/A					
M1L	N/A					
M1W	N/A					
M2W	N/A					
P1P4L	N/A					
P1M2L	N/A					
C1M2L	N/A					
M1M2L	3	5	21.80	2.630	$F_{(5)} = 1.197$, $p=0.324$	$t_5 = -0.073$, $p=0.945$
	2.4	2	21.95	1.90		

Table 5.80. Results from *t* tests of MIS 3 and age group 2.4 of *C. lupus*. *indicates *t* test result with equal variance not assumed, based on significant Levene's test ($p<0.05$) indicating unequal variances. N/A indicates too few individuals for analysis. Significance indicated by $p<0.05$.

- Due to low numbers of individuals, some measurements were unable to be analysed.
- Levene's test not possible for DentaryL due to low number of individuals, questioning *t* test result.
- Levene's test found the remaining measurements to be non-significant and hence, have equal variances.
- *t* tests found all analysed measurements to be non-significant, indicating no differences between Britain and the mainland European sites during MIS 3/age group 2.4. Suggestive of a lack of regional difference between Britain and mainland Europe at this time.

Table 5.81 shows the results from *t* tests between MIS 5e-a in Britain, and the equivalent broad European age group 2.8.

Measure	**MIS/Age group**	**n**	**Mean**	**SD**	**Levene's test**	***t* test**
p4L	5e-a	34	16.70	0.925	$F_{(38)} = 0.403$, $p=0.529$	$t_{38} = 1.444$, $p=0.157$
	2.8	6	16.11	0.933		
p4W	5e-a	34	8.51	0.657	$F_{(38)} = 5.770$, $p=0.021$	$t_{37.355} = 6.227$, $p=0.0001$*
	2.8	6	7.74	0.128		
m1Ltrig	5e-a	24	21.23	1.265	$F_{(30)} = 1.256$, $p=0.271$	$t_{30} = 2.389$, $p=0.023$
	2.8	8	20.07	0.894		
m1Ltal	5e-a	24	7.55	0.562	$F_{(30)} = 0.401$, $p=0.531$	$t_{30} = 0.648$, $p=0.522$
	2.8	8	7.39	0.620		
m1W	5e-a	24	12.14	0.809	$F_{(30)} = 1.097$, $p=0.303$	$t_{30} = 2.541$, $p=0.016$
	2.8	8	11.34	0.646		
m2L	N/A					
m2W	N/A					
p1p4L	5e-a	15	50.62	2.447	$F_{(17)} = 1.027$, $p=0.325$	$t_{17} = -0.786$, $p=0.442$
	2.8	4	51.88	4.203		
p2p4L	5e-a	16	44.11	2.29	$F_{(19)} = 0.023$, $p=0.881$	$t_{19} = -0.620$, $p=0.542$
	2.8	5	44.88	2.90		
p1m3L	N/A					
p2m3L	N/A					

DentaryL	N/A					
p3p4D	5e-a	17	27.88	1.395	$F_{(17)} = 14.230$, $p=0.002$	$t_{1.021} = -0.289$, $p=0.820$*
	2.8	2	28.85	4.702		
p3p4B	5e-a	14	13.44	1.522	$F_{(14)} = 0.547$, $p=0.472$	$t_{14} = 0.161$, $p=0.875$
	2.8	2	13.25	2.319		
m1m2D	N/A					
m1m2B	N/A					
P3L	5e-a	13	16.48	1.134	$F_{(13)} = 3.962$, $p=0.068$	$t_{13} = -1.420$, $p=0.179$
	2.8	2	17.60	0.184		
P4L	5e-a	12	26.33	1.535	$F_{(12)} = 1.805$, $p=0.204$	$t_{12} = -1.568$, $p=0.143$
	2.8	2	28.90	0.382		
P4W	5e-a	12	13.53	1.144	$F_{(12)} = 0.003$, $p=0.958$	$t_{12} = -0.859$, $p=0.407$
	2.8	2	14.29	1.280		
M1L	5e-a	24	16.68	0.897	$F_{(24)} = 0.845$, $p=0.367$	$t_{24} = -1.559$, $p=0.132$
	2.8	2	17.40	0.622		
M1W	5e-a	22	21.58	1.242	$F_{(22)} = 1.145$, $p=0.296$	$t_{22} = -2.707$, $p=0.013$
	2.8	2	24.03	0.686		
M2W	5e-a	10	13.49	0.835	$F_{(10)} = 0.222$, $p=0.648$	$t_{10} = -0.987$, $p=0.347$
	2.8	2	14.15	1.131		
P1P4L	N/A					
P1M2L	N/A					
C1M2L	N/A					
M1M2L	5e-a	11	23.03	1.481	$F_{(11)} = 0.080$, $p=0.782$	$t_{11} = -0.532$, $p=0.605$
	2.8	2	23.63	1.457		

Table 5.81. Results from *t* test of combined MIS 5e-a and age group 2.8 of *C. lupus*. *indicates *t* test result with equal variance not assumed, based on significant Levene's test ($p<0.05$) indicating unequal variances. N/A indicates too few individuals for analysis. Significance indicated by $p<0.05$.

- Analysis of numerous measurements was not possible due to low numbers of individuals.
- Levene's tests found p4W and p3p4D as significant, indicating unequal variances. Subsequent *t* tests of these measurements do not assume equal variances.
- Levene's test found the remaining measurements as non-significant.
- *t* tests found p4W, m1Ltrig, m1W, M1W as significant, indicating differences in these measurements between Britain and the European mainland at this time. This is in contrast to the similarity of measurements between MIS 3/age group 2.8 (Table 5.79).
- *t* tests found the remaining measurements (p4L, m1Ltal, p1p4L, p2p4L, p3p4B, P3L, P4L, P4W, M1L, M1M2L) as non-significant.

Only the measurements of m1Ltrig, m1Ltal and m1W were able to be analysed between MIS 6 and 7 in Britain and the equivalent age group 3 of European sites due to low numbers of individuals. Table 5.82 shows the results.

Measure	Age group	n	Mean	SD	Levene's test	*t* test
m1Ltrig	6-7	13	20.09	1.097	$F_{(14)} = 1.010$, $p=0.332$	$t_{14} = 1.962$, $p=0.070$
	3	3	18.78	0.566		
m1Ltal	6-7	13	7.32	0.823	$F_{(14)} = 0.737$, $p=0.405$	$t_{14} = 0.090$, $p=0.930$
	3	3	7.27	0.522		
m1W	6-7	13	11.28	0.601	$F_{(14)} = 0.255$, $p=0.621$	$t_{14} = 1.548$, $p=0.144$
	3	3	10.65	0.806		

Table 5.82. Results from *t* tests of MIS 6 and 7 in Britain, with the equivalent age group 3 in mainland Europe. Significance indicated by $p<0.05$.

- Levene's test found all measurements as non-significant, indicating equal variances.
- *t* tests were non-significant, indicating that no differences between *C. lupus* from Britain and European mainland at this time.

Summary

Equivalent age groups between Britain and the European mainland were compared. Regional differences were found by tests in p4W, m1Ltrig, m1W and M1W between MIS 5e-a and age group 2.8. It was not possible to analyse numerous measurements due to low number of individuals in the European age groups. It is also important to note that small sample sizes used in the analyses.

In contrast, MIS 3 and the equivalent age group 2.4 were similar, as well as the few possible measurements from MIS 6-7 and the equivalent age group 3. The presence of differences between MIS 5e-a and the equivalent age group 2.8 were expected, as measurements of MIS 5a in Britain were found to be significant. It is therefore possible that the differences seen here are also related to MIS 5a in Britain. Thus, during the early Late Pleistocene, different dietary adaptations were apparent between Britain and Europe.

5.3.4. Climate analysis

Previously, the raw measurements have been investigated for temporal differences. In this section, the measurements will be investigated to see whether differences exist in *C. lupus* between different climatic regimes.

Analysis was based on British *C. lupus* age groups, which were amalgamated into climate-type groupings: group 1, representing cold climates included MIS 3, 5a and 6, group 2, representing warm climates included MIS 5e and 7. Only British material was analysed due to better constrained chronology of sites. Not enough individuals were present in every

measurement to consistently include MIS 2 and MIS 5c, therefore they have been excluded from the analysis. However, some small sample sizes remain present, and their use and associated errors are explained in 5.3.2.

Analysis will involve *t* tests to examine the differences present in the measurements between the two climate groupings. Table 5.83 shows the results.

Measure	Group	n	Mean	SD	Levene's test	*t* test
p4L	1	53	16.50	0.868	$F_{(62)} = 0.639$, $p=0.427$	$t_{62} = 2.001$, $p=0.050$
	2	11	15.94	0.714		
p4W	1	53	8.43	0.588	$F_{(62)} = 1.142$, $p=0.289$	$t_{62} = 2.352$, $p=0.022$
	2	11	7.95	0.753		
m1Ltrig	1	42	21.01	1.245	$F_{(53)} = 0.235$, $p=0.630$	$t_{53} = 2.532$, $p=0.014$
	2	13	20.02	1.172		
m1Ltal	1	41	7.39	0.590	$F_{(52)} = 0.601$, $p=0.442$	$t_{52} = -0.425$, $p=0.673$
	2	13	7.48	0.769		
m1W	1	42	11.96	0.760	$F_{(53)} = 1.379$, $p=0.246$	$t_{53} = 3.106$, $p=0.003$
	2	13	11.24	0.626		
m2L	1	37	11.59	0.697	$F_{(49)} = 1.841$, $p=0.181$	$t_{49} = 1.826$, $p=0.074$
	2	14	11.14	0.994		
m2W	1	35	8.80	0.611	$F_{(47)} = 4.512$, $p=0.039$	$t_{18.427} = 1.529$, $p=0.143$*
	2	14	8.42	0.865		
p1p4L	1	27	50.54	2.734	$F_{(31)} = 2.717$, $p=0.109$	$t_{31} = -0.071$, $p=0.944$
	2	6	50.62	1.435		
p2p4L	1	30	44.24	2.497	$F_{(34)} = 4.163$, $p=0.049$	$t_{15.779} = 0.501$, $p=0.623$*
	2	6	43.91	1.180		
p1m3L	1	14	96.05	4.405	$F_{(17)} = 2.150$, $p=0.161$	$t_{17} = 1.103$, $p=0.285$
	2	5	93.73	2.573		
p2m3L	1	15	89.73	4.185	$F_{(18)} = 0.246$, $p=0.626$	$t_{18} = 0.622$, $p=0.542$
	2	5	88.39	4.148		
DentaryL	N/A					
p3p4D	1	30	27.63	1.401	$F_{(35)} = 1.861$, $p=0.181$	$t_{35} = 1.892$, $p=0.067$
	2	7	26.29	2.690		
p3p4B	1	28	12.93	1.382	$F_{(33)} = 1.429$, $p=0.240$	$t_{33} = 2.499$, $p=0.018$
	2	7	11.55	0.952		
m1m2D	1	27	31.39	2.306	$F_{(34)} = 0.233$, $p=0.633$	$t_{34} = 1.512$, $p=0.140$
	2	9	30.07	2.200		
m1m2B	1	24	13.47	1.341	$F_{(32)} = 0.578$, $p=0.453$	$t_{32} = 2.539$, $p=0.016$
	2	10	12.21	1.246		
P3L	N/A					
P4L	1	18	25.90	1.339	$F_{(20)} = 0.412$, $p=0.528$	$t_{20} = 0.015$, $p=0.988$
	2	4	25.89	1.890		
P4W	1	18	13.38	1.319	$F_{(20)} = 2.193$, $p=0.154$	$t_{20} = -1.409$, $p=0.174$
	2	4	14.35	0.645		
M1L	1	33	16.16	1.034	$F_{(44)} = 0.097$, $p=0.757$	$t_{44} = -0.061$, $p=0.952$
	2	13	16.18	0.949		
M1W	1	31	21.84	1.521	$F_{(39)} = 0.481$, $p=0.492$	$t_{39} = -0.010$, $p=0.992$
	2	10	21.85	1.402		
M2W	1	14	13.67	0.768	$F_{(18)} = 0.138$, $p=0.715$	$t_{18} = 1.031$, $p=0.316$
	2	6	13.27	0.825		
P1P4L	N/A					
P1M2L	N/A					

C1M2L	N/A					
M1M2L	1	16	22.52	1.90	$F_{(19)} = 0.414$, p=0.528	$t_{19} = 0.307$, p=0.762
	2	5	22.23	1.417		

Table 5.83. Results of *t* tests between cold climate group 1 and warm climate group 2. *indicates *t* test result with equal variance not assumed, based on significant Levene's test (p<0.05) indicating unequal variances. N/A indicates too few individuals for analysis. Significance indicated by p<0.05.

- Levene's test found m2W, p2p4L to be significant, indicating unequal variances. Subsequent *t* test results for these measurements do not assume equality.
- Levene's test found remaining measurements to be no-significant, indicating equal variances.
- *t* tests found p4W, m1Ltrig, m1W, p3p4B, m1m2B as significant between the climate groups. These measurements were also temporally significant (Table 5.39).
- Remaining measurements (p4L, m1Ltal, m2L, m2W, p1p4L, p2p4L, p1m3L, p2m3L p3p4D, m1m2D, P4L, P4W, M1L, M1W, M2W, M1M2L) were non-significant, indicating no differences in the majority of measurements between the cold and warm climate groups.

5.3.5. Species differences

In the earlier section (5.3.2) the raw dietary measurements were examined for temporal variation. In this section, the same raw measurements will be analysed by species group to examine whether differences between species are statistically significant.

Modern *C. lupus* was combined with Pleistocene *C. lupus*. The high latitude Swedish wolf dataset was used. The species groups were analysed using one-way ANOVA. As explained in 5.3.2 it is important to note that some analysed measurements contain small sample sizes, particularly for *C. etruscus* and *C. arnensis*. The inclusion of small sample sizes may increase the risk of errors in the analysis, however, efforts to minimise this risk has been taken and the associated issues have been taken as a caveat. Table 5.84 shows the results from Levene's test and one-way ANOVA.

Measure	**Species**	**n**	**mean**	**SD**	**Levene's test**	**one-way ANOVA**
p4L	1	121	16.08	0.877	$F_{(3, 168)} = 1.418$, p=0.239	$F_{(3, 168)} = 82.233$, p=0.0001
	2	24	13.69	0.950		
	3	16	15.12	0.651		
	4	11	13.22	0.484		
p4W	1	120	8.20	0.608	$F_{(3, 166)} = 2.846$, p=0.039	$F_{(3, 166)} = 125.137$, p=0.0001
	2	24	6.28	0.640		
	3	15	6.88	0.401		
	4	11	5.78	0.326		

m1Ltrig	1	117	20.55	1.141	$F_{(3, 163)} = 1.348$, $p=0.261$	$F_{(3, 161)} = 203.038$, $p=0.0001$
	2	26	16.24	1.020		
	3	14	16.94	0.960		
	4	10	14.64	0.635		
m1Ltal	1	116	7.61	0.644	$F_{(3, 166)} = 6.544$, $p=0.0001$	$F_{(3, 166)} = 33.934$, $p=0.0001$
	2	29	6.71	0.393		
	3	15	6.89	0.312		
	4	10	6.29	0.453		
m1W	1	117	11.74	0.724	$F_{(3, 161)} = 2.883$, $p=0.038$	$F_{(3, 161)} = 168.103$, $p=0.0001$
	2	24	9.23	0.616		
	3	15	9.64	0.389		
	4	9	8.36	0.396		
m2L	1	100	11.74	0.798	$F_{(3, 149)} = 0.512$, $p=0.674$	$F_{(3, 149)} = 34.928$, $p=0.0001$
	2	28	10.20	0.894		
	3	15	11.04	0.729		
	4	10	10.15	0.663		
m2W	1	98	8.90	0.635	$F_{(3, 139)} = 1.156$, $p=0.329$	$F_{(3, 139)} = 49.553$, $p=0.0001$
	2	25	7.57	0.687		
	3	12	7.87	0.429		
	4	8	7.08	0.535		
p1p4L	1	85	50.47	2.546	$F_{(3, 110)} = 0.737$, $p=0.532$	$F_{(3, 110)} = 42.347$, $p=0.0001$
	2	12	43.17	1.779		
	3	11	48.30	2.346		
	4	6	43.90	1.688		
p2p4L	1	90	43.84	2.167	$F_{(3, 123)} = 0.639$, $p=0.591$	$F_{(3, 123)} = 43.596$, $p=0.0001$
	2	18	38.22	2.867		
	3	12	41.22	1.997		
	4	7	37.90	1.775		
p1m3L	1	68	95.86	3.227	$F_{(3, 85)} = 0.224$, $p=0.880$	$F_{(3, 85)} = 77.070$, $p=0.0001$
	2	9	82.30	2.657		
	3	8	88.67	4.098		
	4	4	79.59	3.189		
p2m3L	1	68	89.39	3.232	$F_{(3, 91)} = 0.162$, $p=0.921$	$F_{(3, 91)} = 83.147$, $p=0.0001$
	2	12	77.20	3.027		
	3	9	82.41	4.002		
	4	6	73.87	3.396		
p3p4D	1	89	27.93	2.047	$F_{(3. 123)} = 0.379$, $p=0.768$	$F_{(3, 123)} = 121.057$, $p=0.0001$
	2	18	19.68	2.607		
	3	13	21.35	2.436		
	4	7	18.37	2.051		
p3p4B	1	83	12.92	1.263	$F_{(3, 115)} = 2.665$, $p=0.051$	$F_{(3, 115)} = 78.268$, $p=0.0001$
	2	18	9.19	1.245		
	3	13	9.88	1.014		
	4	5	7.99	0.144		
m1m2D	1	82	32.58	2.781	$F_{(3, 114)} = 1.747$, $p=0.161$	$F_{(3, 114)} = 116.781$, $p=0.0001$
	2	15	22.14	2.119		
	3	14	24.56	2.288		
	4	7	21.34	1.900		
m1m2B	1	80	13.10	1.240	$F_{(3, 108)} = 4.968$, $p=0.003$	$F_{(3, 108)} = 58.653$, $p=0.0001$
	2	15	10.01	0.835		
	3	11	10.61	0.321		
	4	6	9.09	0.970		
P3L	1	74	16.10	1.057	$F_{(3, 89)} = 2.333$, $p=0.079$	$F_{(3, 89)} = 36.445$, $p=0.0001$
	2	11	13.55	0.826		

	3	5	14.26	0.134		
	4	3	12.17	0.500		
P4L	1	69	26.43	1.289	$F_{(3, 92)} = 1.920$, $p=0.132$	$F_{(3, 92)} = 78.542$, $p=0.0001$
	2	16	22.57	1.161		
	3	7	22.54	1.239		
	4	4	20.17	0.309		
P4W	1	68	14.14	1.138	$F_{(3, 89)} = 1.034$, $p=0.382$	$F_{(3, 89)} = 58.257$, $p=0.0001$
	2	14	11.00	0.796		
	3	7	11.55	0.853		
	4	4	9.61	0.703		
M1L	1	96	16.70	1.038	$F_{(3, 128)} = 1.913$, $p=0.131$	$F_{(3, 128)} = 77.122$, $p=0.0001$
	2	22	13.60	0.724		
	3	9	15.56	0.652		
	4	5	13.10	0.862		
M1W	1	88	22.57	1.494	$F_{(3, 117)} = 1.928$, $p=0.129$	$F_{(3, 117)} = 57.191$, $p=0.0001$
	2	19	18.66	1.147		
	3	9	20.33	0.985		
	4	5	17.74	0.924		
M2W	1	67	14.17	0.827	$F_{(3, 87)} = 1.054$, $p=0.373$	$F_{(3, 87)} = 35.537$, $p=0.0001$
	2	15	12.13	1.092		
	3	5	12.35	0.745		
	4	4	11.51	0.579		
P1P4L	1	53	64.23	3.318	$F_{(3, 58)} = 1.794$, $p=0.158$	$F_{(3, 58)} = 13.663$, $p=0.0001$
	2	4	57.99	2.658		
	3	2	59.80	1.096		
	4	3	54.39	0.106		
P1M2L	1	50	84.21	3.278	$F_{(3, 53)} = 2.447$, $p=0.096$	$F_{(3, 53)} = 32.912$, $p=0.0001$
	2	3	75.85	2.284		
	3	N/A				
	4	3	70.88	0.580		
C1M2L	1	48	86.88	3.479	$F_{(2, 51)} = 0.330$, $p=0.720$	$F_{(2, 51)} = 31.968$, $p=0.0001$
	2	3	77.36	3.107		
	3	N/A				
	4	3	73.09	2.370		
M1M2L	1	70	23.48	1.525	$F_{(3, 82)} = 1.501$, $p=0.220$	$F_{(3, 82)} = 28.890$, $p=0.0001$
	2	8	19.76	1.253		
	3	4	21.67	2.069		
	4	4	18.23	0.269		

Table 5.84. Results of Levene's test and one-way ANOVA for species groups, indicating number of individuals, mean and standard deviation (SD). Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Levene's test indicated p4W, m1Ltal, m1W and m1m2B as significant, indicating unequal variances. As these measurements are normally distributed, and do not violate the assumption of independence, all were kept in the analysis.
- Levene's test found remaining measurements to be non-significant, indicating equal variances.
- One-way ANOVA found all measurements between the four canids significant.

Post hoc tests were subsequently carried out on all significant measurements to enable multiple comparisons. Tukey HSD was used for measurements with equal variances, and Dunnet's T3 for measurements with unequal variances.

Table 5.85 shows the result of Tukey HSD *post hoc* test of p4L for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	2.38725*	.19016	.0001	1.8938	2.8807
	3	.95870*	.22639	.0001	.3712	1.5462
	4	2.86421*	.26800	.0001	2.1688	3.5597
2	1	-2.38725*	.19016	.0001	-2.8807	-1.8938
	3	-1.42854*	.27467	.0001	-2.1413	-.7158
	4	.47697	.30987	.416	-.3271	1.2810
3	1	-.95870*	.22639	.0001	-1.5462	-.3712
	2	1.42854*	.27467	.0001	.7158	2.1413
	4	1.90551*	.33332	.0001	1.0406	2.7705
4	1	-2.86421*	.26800	.0001	-3.5597	-2.1688
	2	-.47697	.30987	.416	-1.2810	.3271
	3	-1.90551*	.33332	.0001	-2.7705	-1.0406

Table 5.85. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for p4L in the species groups. Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found p4L in *C. lupus* as significantly different from all other analysed species.
- p4L in *C. mosbachensis* p4L was significantly different from *C. etruscus,* and non-significant with *C. arnensis*.
- p4L in *C. etruscus* p4L was significantly different from *C. arnensis*.

Table 5.86 shows the result of Dunnett's T3 *post hoc* test of p4W for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	1.91350*	.14191	.0001	1.5170	2.3100
	3	1.32075*	.11756	.0001	.9844	1.6571
	4	2.42263*	.11283	.0001	2.0906	2.7547
2	1	-1.91350*	.14191	.0001	-2.3100	-1.5170
	3	-.59275*	.16670	.006	-1.0547	-.1308
	4	.50913*	.16340	.022	.0531	.9652
3	1	-1.32075*	.11756	.0001	-1.6571	-.9844
	2	.59275*	.16670	.006	.1308	1.0547
	4	1.10188*	.14276	.0001	.6945	1.5093
4	1	-2.42263*	.11283	.0001	-2.7547	-2.0906
	2	-.50913*	.16340	.022	-.9652	-.0531
	3	-1.10188*	.14276	.0001	-1.5093	-.6945

Table 5.86. Results of *post hoc* one way ANOVA using Dunnett's T3 for multiple comparisons for p4W in the species groups. *Mean difference is significant at 0.05 level.

Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Dunnett's T3 found p4W between all species as significantly different.

Table 5.87 shows the result of Tukey HSD *post hoc* test of m1Ltrig for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	4.31009*	.23578	.0001	3.6981	4.9221
	3	3.60976*	.30754	.0001	2.8115	4.4080
	4	5.90947*	.35829	.0001	4.9795	6.8395
2	1	-4.31009*	.23578	.0001	-4.9221	-3.6981
	3	-.70033	.36050	.214	-1.6361	.2354
	4	1.59938*	.40465	.001	.5490	2.6498
3	1	-3.60976*	.30754	.0001	-4.4080	-2.8115
	2	.70033	.36050	.214	-.2354	1.6361
	4	2.29971*	.45026	.0001	1.1310	3.4685
4	1	-5.90947*	.35829	.0001	-6.8395	-4.9795
	2	-1.59938*	.40465	.001	-2.6498	-.5490
	3	-2.29971*	.45026	.0001	-3.4685	-1.1310

Table 5.87. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for m1Ltrig in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found m1Ltrig in *C. lupus* as significantly different from all other analysed species.
- m1Ltrig in *C. mosbachensis* was significantly different from *C. arnensis*, and non-significant with *C. etruscus*.
- m1Ltrig in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.88 shows the result of Dunnett's T3 *post hoc* test of m1Ltal for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	.89810*	.09442	.0001	.6429	1.1533
	3	.72291*	.10043	.0001	.4426	1.0032
	4	1.32024*	.15517	.0001	.8425	1.7979
2	1	-.89810*	.09442	.0001	-1.1533	-.6429
	3	-.17520	.10884	.507	-.4778	.1274
	4	.42214	.16074	.105	-.0637	.9080
3	1	-.72291*	.10043	.0001	-1.0032	-.4426
	2	.17520	.10884	.507	-.1274	.4778
	4	.59733*	.16434	.014	.1039	1.0908
4	1	-1.32024*	.15517	.0001	-1.7979	-.8425
	2	-.42214	.16074	.105	-.9080	.0637
	3	-.59733*	.16434	.014	-1.0908	-.1039

Table 5.88. Results of *post hoc* one way ANOVA using Dunnett's T3 for multiple comparisons for m1Ltal in the species groups. *Mean difference is significant at 0.05 level.

Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Dunnett's T3 found m1Ltal in *C. lupus* as significantly different from all other analysed species.
- m1Ltal in *C. mosbachensis* was non-significant with both *C. etruscus* and *C. arnensis.*
- m1Ltal in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.89 shows the result of Dunnett's T3 *post hoc* test of m1W for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	2.50347*	.14253	.0001	2.1087	2.8983
	3	2.09356*	.12063	.0001	1.7541	2.4330
	4	3.37222*	.14811	.0001	2.9174	3.8271
2	1	-2.50347*	.14253	.0001	-2.8983	-2.1087
	3	-.40992	.16093	.085	-.8558	.0360
	4	.86875*	.18244	.001	.3461	1.3914
3	1	-2.09356*	.12063	.0001	-2.4330	-1.7541
	2	.40992	.16093	.085	-.0360	.8558
	4	1.27867*	.16589	.0001	.7886	1.7687
4	1	-3.37222*	.14811	.0001	-3.8271	-2.9174
	2	-.86875*	.18244	.001	-1.3914	-.3461
	3	-1.27867*	.16589	.0001	-1.7687	-.7886

Table 5.89. Results of *post hoc* one way ANOVA using Dunnett's T3 for multiple comparisons for m1W in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Dunnett's T3 found m1W in *C. lupus* as significantly different from all other analysed species.
- m1W in *C. mosbachensis* was significantly different from *C. arnensis*, and non-significant with *C. etruscus*.
- m1W in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.90 shows the result of Tukey HSD *post hoc* test of m2L for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	1.53989*	.17169	.0001	1.0938	1.9860
	3	.70260*	.22234	.010	.1249	1.2803
	4	1.59460*	.26632	.0001	.9026	2.2866
2	1	-1.53989*	.17169	.0001	-1.9860	-1.0938
	3	-.83729*	.25693	.007	-1.5049	-.1697
	4	.05471	.29582	.998	-.7139	.8233
3	1	-.70260*	.22234	.010	-1.2803	-.1249

	2	.83729*	.25693	.007	.1697	1.5049
	4	.89200*	.32782	.036	.0402	1.7438
4	1	-1.59460*	.26632	.0001	-2.2866	-.9026
	2	-.05471	.29582	.998	-.8233	.7139
	3	-.89200*	.32782	.036	-1.7438	-.0402

Table 5.90. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for m2L in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found m2L in *C. lupus* as significantly different from all other analysed species.
- m2L in *C. mosbachensis* was significantly different from *C. etruscus*, yet non-significant with to *C. arnensis*.
- m2L in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.91 shows the result of Tukey HSD *post hoc* test of m2W for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	1.32991*	.14020	.0001	.9653	1.6945
	3	1.02864*	.19137	.0001	.5310	1.5263
	4	1.82406*	.23007	.0001	1.2258	2.4223
2	1	-1.32991*	.14020	.0001	-1.6945	-.9653
	3	-.30127	.21974	.520	-.8727	.2701
	4	.49415	.25416	.215	-.1668	1.1551
3	1	-1.02864*	.19137	.0001	-1.5263	-.5310
	2	.30127	.21974	.520	-.2701	.8727
	4	.79542*	.28560	.031	.0528	1.5381
4	1	-1.82406*	.23007	.0001	-2.4223	-1.2258
	2	-.49415	.25416	.215	-1.1551	.1668
	3	-.79542*	.28560	.031	-1.5381	-.0528

Table 5.91. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for m2W in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found m2L in *C. lupus* as significantly different from all other analysed species.
- m2W in *C. mosbachensis* was non-significant with both *C. etruscus* and *C. arnensis*.
- m2W in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.92 shows the result of Tukey HSD *post hoc* test of p1p4L for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	7.29375*	.74885	.0001	5.3402	9.2473
	3	2.16359*	.77811	.032	.1337	4.1935
	4	6.56375*	1.02576	.0001	3.8878	9.2397
2	1	-7.29375*	.74885	.0001	-9.2473	-5.3402

	3	-5.13015*	1.01365	.0001	-7.7745	-2.4858
	4	-.73000	1.21417	.931	-3.8975	2.4375
3	1	-2.16359*	.77811	.032	-4.1935	-.1337
	2	5.13015*	1.01365	.0001	2.4858	7.7745
	4	4.40015*	1.23243	.003	1.1851	7.6152
4	1	-6.56375*	1.02576	.0001	-9.2397	-3.8878
	2	.73000	1.21417	.931	-2.4375	3.8975
	3	-4.40015*	1.23243	.003	-7.6152	-1.1851

Table 5.92. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for p1p4L in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found p1p4L in *C. lupus* as significantly different from all other analysed species.
- p1p4L in *C. mosbachensis* was significantly different from *C. etruscus*, yet non-significant with *C. arnensis*.
- p1p4L in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.93 shows the result of Tukey HSD *post hoc* test of p2p4L for the four canids.

					95% Confidence Interval	
Species	**Species**	**Mean Difference**	**Std. Error**	**Sig.**	**Lower Bound**	**Upper Bound**
1	2	5.62456*	.57993	.0001	4.1141	7.1350
	3	2.62039*	.69026	.001	.8226	4.4182
	4	5.94170*	.88133	.0001	3.6463	8.2371
2	1	-5.62456*	.57993	.0001	-7.1350	-4.1141
	3	-3.00417*	.83706	.003	-5.1843	-.8240
	4	.31714	1.00048	.989	-2.2886	2.9229
3	1	-2.62039*	.69026	.001	-4.4182	-.8226
	2	3.00417*	.83706	.003	.8240	5.1843
	4	3.32131*	1.06822	.012	.5391	6.1035
4	1	-5.94170*	.88133	.0001	-8.2371	-3.6463
	2	-.31714	1.00048	.989	-2.9229	2.2886
	3	-3.32131*	1.06822	.012	-6.1035	-.5391

Table 5.93. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for p2p4L in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found p2p4L in *C. lupus* as significantly different from all other analysed species.
- p2p4L in *C. mosbachensis* was significantly different from *C. etruscus*, yet non-significant with *C. arnensis*.
- p2p4L in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.94 shows the result of Tukey HSD *post hoc* test of p1m3L for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	13.55670*	1.15551	.0001	10.5286	16.5848
	3	7.18184*	1.21762	.0001	3.9910	10.3727
	4	16.27059*	1.67604	.0001	11.8784	20.6628
2	1	-13.55670*	1.15551	.0001	-16.5848	-10.5286
	3	-6.37486*	1.58293	.001	-10.5231	-2.2267
	4	2.71389	1.95760	.511	-2.4162	7.8440
3	1	-7.18184*	1.21762	.0001	-10.3727	-3.9910
	2	6.37486*	1.58293	.001	2.2267	10.5231
	4	9.08875*	1.99489	.0001	3.8610	14.3165
4	1	-16.27059*	1.67604	.0001	-20.6628	-11.8784
	2	-2.71389	1.95760	.511	-7.8440	2.4162
	3	-9.08875*	1.99489	.0001	-14.3165	-3.8610

Table 5.94. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for p1m3L in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found p1m3L in *C. lupus* as significantly different from all other analysed species.
- p1m3L in *C. mosbachensis* was significantly different from *C. etruscus*, yet non-significant with *C. arnensis*.
- p1m3L in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.95 shows the result of Tukey HSD *post hoc* test of p2m3L for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	12.18451*	1.03087	.0001	9.4866	14.8825
	3	6.97507*	1.16782	.0001	3.9187	10.0314
	4	15.51951*	1.40214	.0001	11.8499	19.1891
2	1	-12.18451*	1.03087	.0001	-14.8825	-9.4866
	3	-5.20944*	1.45179	.003	-9.0090	-1.4099
	4	3.33500	1.64617	.186	-.9733	7.6433
3	1	-6.97507*	1.16782	.0001	-10.0314	-3.9187
	2	5.20944*	1.45179	.003	1.4099	9.0090
	4	8.54444*	1.73522	.0001	4.0031	13.0858
4	1	-15.51951*	1.40214	.0001	-19.1891	-11.8499
	2	-3.33500	1.64617	.186	-7.6433	.9733
	3	-8.54444*	1.73522	.0001	-13.0858	-4.0031

Table 5.95. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for p2m3L in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found p2m3L in *C. lupus* as significantly different from all other analysed species.
- p2m3L in *C. mosbachensis* was significantly different from *C. etruscus*, yet similar to *C. arnensis*.

- p2m3L in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.96 shows the result of Tukey HSD *post hoc* test of p3p4D for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	8.25098*	.56151	.0001	6.7885	9.7134
	3	6.57589*	.64511	.0001	4.8957	8.2561
	4	9.56106*	.85289	.0001	7.3397	11.7824
2	1	-8.25098*	.56151	.0001	-9.7134	-6.7885
	3	-1.67509	.79081	.153	-3.7348	.3846
	4	1.31008	.96780	.531	-1.2106	3.8307
3	1	-6.57589*	.64511	.0001	-8.2561	-4.8957
	2	1.67509	.79081	.153	-.3846	3.7348
	4	2.98516*	1.01858	.021	.3323	5.6381
4	1	-9.56106*	.85289	.0001	-11.7824	-7.3397
	2	-1.31008	.96780	.531	-3.8307	1.2106
	3	-2.98516*	1.01858	.021	-5.6381	-.3323

Table 5.96. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for p3p4D in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found p3p4D in *C. lupus* as significantly different from all other analysed species ($p<0.05$).
- p3p4D in *C. mosbachensis* was non-significant with both *C. etruscus* and *C. arnensis.*
- p3p4D in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.97 shows the result of Tukey HSD *post hoc* test of p3p4B for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	3.72646*	.31582	.0001	2.9031	4.5498
	3	3.03744*	.36231	.0001	2.0929	3.9820
	4	4.92190*	.55934	.0001	3.4637	6.3801
2	1	-3.72646*	.31582	.0001	-4.5498	-2.9031
	3	-.68902	.44211	.406	-1.8416	.4636
	4	1.19544	.61404	.215	-.4054	2.7963
3	1	-3.03744*	.36231	.0001	-3.9820	-2.0929
	2	.68902	.44211	.406	-.4636	1.8416
	4	1.88446*	.63920	.020	.2181	3.5508
4	1	-4.92190*	.55934	.0001	-6.3801	-3.4637
	2	-1.19544	.61404	.215	-2.7963	.4054
	3	-1.88446*	.63920	.020	-3.5508	-.2181

Table 5.97. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for p3p4B in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found p3p4B in *C. lupus* as significantly different from all other analysed species.

- p3p4B in *C. mosbachensis* was non-significant with both *C. etruscus* and *C. arnensis.*
- p3p4B in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.98 shows the result of Tukey HSD *post hoc* test of m1m2D for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	10.43907*	.73416	.0001	8.5249	12.3533
	3	8.01279*	.75600	.0001	6.0416	9.9839
	4	11.23707*	1.02943	.0001	8.5530	13.9211
2	1	-10.43907*	.73416	.0001	-12.3533	-8.5249
	3	-2.42629	.97151	.066	-4.9593	.1068
	4	.79800	1.19667	.909	-2.3221	3.9181
3	1	-8.01279*	.75600	.0001	-9.9839	-6.0416
	2	2.42629	.97151	.066	-.1068	4.9593
	4	3.22429*	1.21019	.043	.0689	6.3797
4	1	-11.23707*	1.02943	.0001	-13.9211	-8.5530
	2	-.79800	1.19667	.909	-3.9181	2.3221
	3	-3.22429*	1.21019	.043	-6.3797	-.0689

Table 5.98. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for m1m2D in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found m1m2D in *C. lupus* as significantly different from all other analysed species.
- m1m2D in *C. mosbachensis* was non-significant with both *C. etruscus* and *C. arnensis.*
- m1m2D in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.99 shows the result of Dunnett's T3 *post hoc* test of m1m2B for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	3.09504*	.25623	.0001	2.3715	3.8186
	3	2.49056*	.16904	.0001	2.0316	2.9495
	4	4.01571*	.41962	.0001	2.5025	5.5289
2	1	-3.09504*	.25623	.0001	-3.8186	-2.3715
	3	-.60448	.23622	.103	-1.2920	.0830
	4	.92067	.45090	.320	-.5897	2.4311
3	1	-2.49056*	.16904	.0001	-2.9495	-2.0316
	2	.60448	.23622	.103	-.0830	1.2920
	4	1.52515	.40771	.051	-.0057	3.0560
4	1	-4.01571*	.41962	.0001	-5.5289	-2.5025
	2	-.92067	.45090	.320	-2.4311	.5897
	3	-1.52515	.40771	.051	-3.0560	.0057

Table 5.99. Results of *post hoc* one way ANOVA using Dunnett's T3 for multiple comparisons for m1m2B in the species groups. *Mean difference is significant at 0.05 level.

Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Dunnett's T3 found m1m2B in *C. lupus* as significantly different from all other analysed species.
- m1m2B in *C. mosbachensis* was non-significant with *C. etruscus* and *C. arnensis.*
- m1m2B in *C. etruscus* was non-significant with *C. arnensis*.

Table 5.100 shows the result of Tukey HSD *post hoc* test of P3L for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	2.55529*	.32310	.0001	1.7093	3.4013
	3	1.84657*	.46201	.001	.6369	3.0562
	4	3.93257*	.58886	.0001	2.3908	5.4743
2	1	-2.55529*	.32310	.0001	-3.4013	-1.7093
	3	-.70873	.53929	.556	-2.1207	.7033
	4	1.37727	.65125	.156	-.3279	3.0824
3	1	-1.84657*	.46201	.001	-3.0562	-.6369
	2	.70873	.53929	.556	-.7033	2.1207
	4	2.08600*	.73020	.027	.1742	3.9978
4	1	-3.93257*	.58886	.0001	-5.4743	-2.3908
	2	-1.37727	.65125	.156	-3.0824	.3279
	3	-2.08600*	.73020	.027	-3.9978	-.1742

Table 5.100. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for P3L in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found P3L in *C. lupus* as significantly different from all other analysed species.
- P3L in *C. mosbachensis* was non-significant with *C. etruscus* and *C. arnensis*.
- P3L in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.101 shows the result of Tukey HSD *post hoc* test of P4L for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	3.85730*	.34553	.0001	2.9532	4.7614
	3	3.88569*	.49396	.0001	2.5932	5.1782
	4	6.26355*	.64042	.0001	4.5878	7.9393
2	1	-3.85730*	.34553	.0001	-4.7614	-2.9532
	3	.02839	.56430	1.000	-1.4482	1.5050
	4	2.40625*	.69611	.005	.5848	4.2277
3	1	-3.88569*	.49396	.0001	-5.1782	-2.5932
	2	-.02839	.56430	1.000	-1.5050	1.4482
	4	2.37786*	.78050	.016	.3356	4.4201
4	1	-6.26355*	.64042	.0001	-7.9393	-4.5878
	2	-2.40625*	.69611	.005	-4.2277	-.5848

	3	-2.37786*	.78050	.016	-4.4201	-.3356

Table 5.101. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for P4L in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found P4L in *C. lupus* as significantly different from all other analysed species.
- P4L in *C. mosbachensis* was significantly different from *C. arnensis*, yet similar to *C. etruscus*.
- P4L in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.102 shows the result of Tukey HSD *post hoc* test of P4W for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	3.14353*	.31253	.0001	2.3253	3.9618
	3	2.59139*	.42270	.0001	1.4847	3.6981
	4	4.53103*	.54788	.0001	3.0966	5.9655
2	1	-3.14353*	.31253	.0001	-3.9618	-2.3253
	3	-.55214	.49294	.678	-1.8428	.7385
	4	1.38750	.60373	.106	-.1932	2.9682
3	1	-2.59139*	.42270	.0001	-3.6981	-1.4847
	2	.55214	.49294	.678	-.7385	1.8428
	4	1.93964*	.66745	.023	.1921	3.6872
4	1	-4.53103*	.54788	.0001	-5.9655	-3.0966
	2	-1.38750	.60373	.106	-2.9682	.1932
	3	-1.93964*	.66745	.023	-3.6872	-.1921

Table 5.102. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for P4W in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found P4W in *C. lupus* as significantly different from all other analysed species.
- P4W in *C. mosbachensis* was non-significant with both *C. etruscus* and *C. arnensis*.
- P4W in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.103 shows the result of Tukey HSD *post hoc* test of M1L for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	3.09223*	.22869	.0001	2.4969	3.6875
	3	1.13233*	.33729	.006	.2543	2.0103
	4	3.60077*	.44382	.0001	2.4455	4.7561
2	1	-3.09223*	.22869	.0001	-3.6875	-2.4969
	3	-1.95990*	.38283	.0001	-2.9565	-.9633
	4	.50855	.47934	.714	-.7392	1.7563
3	1	-1.13233*	.33729	.006	-2.0103	-.2543
	2	1.95990*	.38283	.0001	.9633	2.9565

	4	2.46844*	.53966	.0001	1.0637	3.8732
4	1	-3.60077*	.44382	.0001	-4.7561	-2.4455
	2	-.50855	.47934	.714	-1.7563	.7392
	3	-2.46844*	.53966	.0001	-3.8732	-1.0637

Table 5.103. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for M1L in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found M1L in *C. lupus* as significantly different from all other analysed species.
- M1L in *C. mosbachensis* was significantly different from *C. etruscus,* yet similar to *C. arnensis*.
- M1L in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.104 shows the result of Tukey HSD *post hoc* test of M1W for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	3.90606*	.35386	.0001	2.9838	4.8283
	3	2.24080*	.48954	.0001	.9649	3.5167
	4	4.83280*	.64310	.0001	3.1567	6.5089
2	1	-3.90606*	.35386	.0001	-4.8283	-2.9838
	3	-1.66526*	.56604	.020	-3.1405	-.1900
	4	.92674	.70308	.553	-.9057	2.7592
3	1	-2.24080*	.48954	.0001	-3.5167	-.9649
	2	1.66526*	.56604	.020	.1900	3.1405
	4	2.59200*	.78023	.006	.5585	4.6255
4	1	-4.83280*	.64310	.0001	-6.5089	-3.1567
	2	-.92674	.70308	.553	-2.7592	.9057
	3	-2.59200*	.78023	.006	-4.6255	-.5585

Table 5.104. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for M1W in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found M1W in *C. lupus* as significantly different from all other analysed species.
- M1W in *C. mosbachensis* was significantly different from *C. etruscus,* yet similar to *C. arnensis*.
- M1W in *C. etruscus* was significantly different from *C. arnensis*.

Table 5.105 shows the result of Tukey HSD *post hoc* test of M2W for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	2.04440*	.24709	.0001	1.3972	2.6916
	3	1.82573*	.40102	.0001	.7753	2.8762
	4	2.66373*	.44523	.0001	1.4975	3.8300

2	1	-2.04440*	.24709	.0001	-2.6916	-1.3972
	3	-.21867	.44669	.961	-1.3887	.9514
	4	.61933	.48677	.583	-.6557	1.8944
3	1	-1.82573*	.40102	.0001	-2.8762	-.7753
	2	.21867	.44669	.961	-.9514	1.3887
	4	.83800	.58027	.476	-.6820	2.3580
4	1	-2.66373*	.44523	.0001	-3.8300	-1.4975
	2	-.61933	.48677	.583	-1.8944	.6557
	3	-.83800	.58027	.476	-2.3580	.6820

Table 5.105. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for M2W in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found M2W in *C. lupus* as significantly different from all other analysed species.
- M2W in *C. mosbachensis* was non-significant with both *C. etruscus* and *C. arnensis*.
- M2W in *C. etruscus* was non-significant with *C. arnensis*.

Table 5.106 shows the result of Tukey HSD *post hoc* test of P1P4L for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	6.24066*	1.66063	.002	1.8481	10.6332
	3	4.43066	2.30691	.231	-1.6714	10.5327
	4	9.83233*	1.90063	.0001	4.8049	14.8597
2	1	-6.24066*	1.66063	.002	-10.6332	-1.8481
	3	-1.81000	2.77354	.914	-9.1463	5.5263
	4	3.59167	2.44603	.463	-2.8783	10.0617
3	1	-4.43066	2.30691	.231	-10.5327	1.6714
	2	1.81000	2.77354	.914	-5.5263	9.1463
	4	5.40167	2.92356	.262	-2.3315	13.1348
4	1	-9.83233*	1.90063	.0001	-14.8597	-4.8049
	2	-3.59167	2.44603	.463	-10.0617	2.8783
	3	-5.40167	2.92356	.262	-13.1348	2.3315

Table 5.106. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for P1P4L in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found P1P4L in *C. lupus* as significantly different from *C. mosbachensis* and *C. arnensis*, yet similar to *C. etruscus*.
- P1P4L in *C. mosbachensis* was non-significant with both *C. etruscus* and *C. arnensis*.
- P1P4L in *C. etruscus* was non-significant with *C. arnensis*.

Table 5.107 shows the result of Tukey HSD *post hoc* test of P1M2L for the three canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	8.36673*	1.89346	.0001	3.8011	12.9324

	4	13.33673*	1.89346	.0001	8.7711	17.9024
2	1	-8.36673*	1.89346	.0001	-12.9324	-3.8011
	4	4.97000	2.60087	.146	-1.3014	11.2414
4	1	-13.33673*	1.89346	.0001	-17.9024	-8.7711
	2	-4.97000	2.60087	.146	-11.2414	1.3014

Table 5.107. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for P1M2L in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- *C. etruscus* was not analysed as only one individual for P1M2L.
- Tukey HSD found P1M2L in *C. lupus* to be significantly different from *C. mosbachensis* and *C. arnensis*.
- P1M2L in *C. mosbachensis* was non-significant with *C. arnensis*.

Table 5.108 shows the result of Tukey HSD *post hoc* test of C1M2L for the three canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	9.51521*	2.04026	.0001	4.5901	14.4404
	4	13.78854*	2.04026	.0001	8.8634	18.7137
2	1	-9.51521*	2.04026	.0001	-14.4404	-4.5901
	4	4.27333	2.79922	.287	-2.4839	11.0306
4	1	-13.78854*	2.04026	.0001	-18.7137	-8.8634
	2	-4.27333	2.79922	.287	-11.0306	2.4839

Table 5.108. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for C1M2L in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- *C. etruscus* not analysed due to having one individual for C1M2L.
- Tukey HSD found C1M2L in *C. lupus* to be significantly different from both *C. mosbachensis* and *C. arnensis*.
- C1M2L in *C. mosbachensis* was non-significant with *C. arnensis*.

Table 5.109 shows the result of Tukey HSD *post hoc* test of M1M2L for the four canids.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	3.72211*	.55987	.0001	2.2539	5.1904
	3	1.81586	.77120	.094	-.2066	3.8383
	4	5.24836*	.77120	.0001	3.2259	7.2708
2	1	-3.72211*	.55987	.0001	-5.1904	-2.2539
	3	-1.90625	.91864	.170	-4.3154	.5029
	4	1.52625	.91864	.351	-.8829	3.9354
3	1	-1.81586	.77120	.094	-3.8383	.2066
	2	1.90625	.91864	.170	-.5029	4.3154
	4	3.43250*	1.06076	.009	.6507	6.2143
4	1	-5.24836*	.77120	.0001	-7.2708	-3.2259
	2	-1.52625	.91864	.351	-3.9354	.8829

	3	-3.43250*	1.06076	.009	-6.2143	-.6507

Table 5.109. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for M1M2L in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found M1M2L in *C. lupus* to be significantly different from both *C. mosbachensis* and *C. arnensis*, yet non-significant with *C. etruscus*.
- M1M2L in *C. mosbachensis* was non-significant with *C. etruscus* and *C. arnensis*.
- M1M2L in *C. etruscus* was significantly different from *C. arnensis*.

Summary

Sample sizes were often small for measurements of *C. etruscus* and *C. arnensis*. Although homogeneity of variances was assessed throughout, an increased risk of errors remained present for some analyses.

C. lupus was significantly different from *C. mosbachensis*, *C. etruscus* and *C. arnensis* in the majority of measurements, except P1P4L and M1M2L, where it was most similar to *C. etruscus*. *C. lupus* had the highest amount of differences out of all the species.

C. mosbachensis was significantly different from *C. lupus* in all measurements but shared similarities with both *C. etruscus* and *C. arnensis*.

C. mosbachensis was different from *C. etruscus* in p4L, p4W, m2L, p1p4L, p2p4L, p1m3L, p2m3L, M1L, M1W, but was similar in m1Ltrig, m1Ltal, m1W, m2W, p3p4D, p3p4B, m1m2D, m1m2B, P3L, P4L, P4W, M2W, P1P4L, M1M2L.

C. mosbachensis was different from *C. arnensis* in p4W, m1Ltrig, m1W, P4L, but was similar in p4L, m1Ltal, m2L, m2W, p1p4L, p2p4L, p1m3L, p2m3L, p3p4D, p3p4B, m1m2D, m1m2B, P3L, P4W, M1L, M1W, M2W, P1P4L, P1M2L, C1M2L, M1M2L.

C. etruscus was significantly different from *C. arnensis* in most measurements; p4L, p4W, m1Ltrig, m1Ltal, m1W, m2L, m2W, p1p4L, p2p4L, p1m3L, p2m3L, p3p4D, p3p4B, P3L, P4L, M1L, M1W, M1M2L. However, they are similar in m1m2D, m1m2B, M2W, P1P4L.

C. etruscus was not analysed for P1M2L and C1M2L due to low numbers of individuals.

5.3.6. Stepwise Discriminant Function Analysis

Stepwise Discriminant Function Analysis (DFA) was used to investigate how well the dietary measurements could discriminate between 1). the chronological groupings of *C. lupus* in

Britain and 2). the different canid species groups. By predicting group membership, it is possible to examine whether differences are temporally or species related. This is accomplished by estimating the relationship between the dependent variable (e.g. group age, species) and a set of independent variables (raw dietary measurements).

Due to low numbers of individuals the following measurements were also not possible to include; p1m3L, p2m3L, DentaryL, C1M2L and P1M2L.

5.3.6.1. Stepwise Discriminant Function Analysis: age groups

Discriminant analysis was performed on age groups MIS 1, 3, 5a and 7, with MIS 1 represented by the modern Swedish *C. lupus* dataset, and the MIS 3, 5a and 7 individuals from Britain.

To assess the predictive ability of the measurements, tests of equality of group means were carried out by Wilks' Lambda and ANOVA (F test) to test the mean differences. The results are shown in Table 5.110.

	Wilks' Lambda	F	df1	df2	Sig.
m1L	.799	8.323	3	99	.0001
m1W	.739	11.652	3	99	.0001
m1Ltrig	.763	10.270	3	99	.0001
m1Ltal	.847	5.956	3	99	.001
p4L	.619	20.343	3	99	.0001
p4W	.827	6.880	3	99	.0001
m2L	.779	9.368	3	99	.0001
m2W	.813	7.604	3	99	.0001
p1p4L	.980	.664	3	99	.576
p2p4L	.886	4.230	3	99	.007
p1m3L	.843	6.152	3	99	.001
p2m3L	.930	2.473	3	99	.066
p3p4D	.889	4.116	3	99	.009
p3p4B	.699	14.188	3	99	.0001
m1m2D	.585	23.382	3	99	.0001
m1m2B	.717	13.055	3	99	.0001
UP3L	.940	2.106	3	99	.104
UP4L	.736	11.854	3	99	.0001
UP4W	.710	13.450	3	99	.0001
UM1L	.635	18.985	3	99	.0001
UM1W	.633	19.107	3	99	.0001
UM2W	.605	21.525	3	99	.0001
UM1M2L	.534	28.830	3	99	.0001

Table 5.110. Results from Wilks' Lambda and tests of equality of group means using ANOVA. Temporal DFA using MIS 1, 3, 5a and 7 *C. lupus*.

All measurements have relatively high Wilks' Lambda values, potentially indicating less effective contributions to the analysis. From the F test, p1p4L, p2m3L and P3L were found

as non-significant (p>0.05) in their group differences, indicating their lower predictive abilities in comparison to the majority of significant measurements (p<0.05), which have strong predictive ability.

Correlations between measurements were assessed, with high and positive correlations indicated by results close to 1.0, while little or no correlation is indicated by results close to 0. The highest correlated measurements were m1L and m1W (0.730), m1L and m1Ltrig (0.816), m1Ltrig and m1W (0.719) and p1m3L and p2m3L (0.776). The remaining correlated measurements were closer to 0.5 and included: p4L and p4W (0.608), p3p4D and p3p4B (0.620), p3p4D and m1m2D (0.554). These are more moderate correlations.

Box's M was employed to test the equality of covariances in the groups. The log determinants measure the variability of the age groups, and hence for the assumption of equality to be met, the log determinants should be similar. Table 5.111 shows the results.

Age	Rank	Log Determinant
1	11	-.720
3	11	-5.709
5a	11	-3.329
7	.[a]	.[b]
Pooled within-groups	11	1.467

Table 5.111. The log determinants for MIS 1, 3, 5a and 7 for the temporal analysis DFA of *C. lupus*. Ranks and natural logarithms of determinants are those of the group covariance matrices. a. Rank < 10, b. The DFA found too few cases for it to be non-singular.

Log determinants for MIS 3 and 5a were broadly similar. MIS 7 was considered singular likely due to low number of cases. The difference in log values between MIS 1 with 3 and 7 suggests differing covariance matrices, which may relate to the sample size differences between the age groups.

Box's M was significant (Box's M = 461.666, $F_{(132,\ 11527.426)}$ = 2.793, p=0.0001), indicating the covariance matrices indeed differ. Box's M can be overly sensitive to large samples, as well as to deviations in multivariate normality, however as the measurements are univariate normal, it is a likely assumption that they are also multivariate normal (Tabachnick and Fidell, 1996). Nonetheless, some minor deviations in kurtosis and skewness may also be present and having an effect. The significant Box's M is likely due to problems with MIS 1 and 7, as indicated by the log determinants (Table 5.111). This will be taken as a caveat in the analysis.

Table 5.112 shows the result from the stepwise selection of measurements used in the DFA based on how much they lower Wilks' Lambda.

Step	Entered	Wilks' Lambda											
						Exact F				Approximate F			
		Statistic	df1	df2	df3	Statistic	df1	df2	Sig.	Statistic	df1	df2	Sig.
1	UM1M2L	.534	1	3	99.000	28.830	3	99.000	.0001				
2	p4L	.340	2	3	99.000	23.383	6	196.000	.0001				
3	UM1W	.210	3	3	99.000					23.603	9	236.223	.0001
4	m1m2D	.149	4	3	99.000					22.299	12	254.284	.0001
5	m1m2B	.118	5	3	99.000					20.424	15	262.655	.0001
6	UP4W	.088	6	3	99.000					20.193	18	266.357	.0001
7	p1m3L	.073	7	3	99.000					18.952	21	267.596	.0001
8	p3p4D	.064	8	3	99.000					17.637	24	267.429	.0001
9	p3p4B	.054	9	3	99.000					16.980	27	266.409	.0001
10	p1p4L	.047	10	3	99.000					16.122	30	264.844	.0001
11	m1L	.041	11	3	99.000					15.618	33	262.914	.0001

Table 5.112. Steps taken by the stepwise method in the DFA. Measurements shown are those entered in the 11 steps. At each step, the variable that minimises the overall Wilks' Lambda is entered. a. Maximum number of steps is 46, b. Minimum partial F to enter is 3.84, c. Maximum partial F to remove is 2.71, d. F level, tolerance, or VIN insufficient for further computation.

In total 11 steps were taken, entering only measurements that lowered Wilks' Lambda including M1M2L, p4L, M1W, m1m2D, m1m2B, P4W, p1m3L, p3p4D, p3p4B, p1p4L, and m1L.

Table 5.113 also shows the number of steps and the measurements selected per step, as well as their tolerance, F to remove value and Wilks' Lambda. Tolerance is the proportion of variance not accounted for by the other independent variables. A variable with low tolerance contributes little to the model, and may be of concern if <0.40. As Table 5.113 shows, all measurements selected are >0.40 in tolerance.

Step		Tolerance	F to Remove	Wilks' Lambda
1	UM1M2L	1.000	28.830	
2	UM1M2L	.996	26.828	.619
	p4L	.996	18.662	.534
3	UM1M2L	.802	24.403	.368
	p4L	.908	22.922	.359
	UM1W	.735	19.993	.340
4	UM1M2L	.801	18.033	.233
	p4L	.856	25.701	.269
	UM1W	.707	17.590	.231
	m1m2D	.868	13.005	.210
5	UM1M2L	.790	18.559	.188
	p4L	.843	18.449	.187
	UM1W	.690	18.547	.188
	m1m2D	.801	10.670	.158
	m1m2B	.828	8.264	.149
6	UM1M2L	.775	18.380	.139
	p4L	.843	16.022	.133
	UM1W	.687	16.346	.133
	m1m2D	.800	10.512	.117
	m1m2B	.713	13.468	.125
	UP4W	.813	10.965	.118
7	UM1M2L	.767	17.991	.115
	p4L	.842	14.692	.108
	UM1W	.660	16.549	.112
	m1m2D	.736	11.857	.101
	m1m2B	.713	11.128	.099
	UP4W	.750	14.169	.106
	p1m3L	.738	6.201	.088
8	UM1M2L	.673	22.907	.111
	p4L	.840	14.571	.094
	UM1W	.614	19.060	.103
	m1m2D	.565	14.011	.093
	m1m2B	.710	11.203	.087
	UP4W	.733	13.721	.092
	p1m3L	.704	5.738	.076
	p3p4D	.549	4.451	.073
9	UM1M2L	.652	24.138	.097
	p4L	.796	13.806	.078

	UM1W	.612	18.284	.086
	m1m2D	.553	11.345	.074
	m1m2B	.674	5.923	.064
	UP4W	.732	13.187	.077
	p1m3L	.672	6.983	.066
	p3p4D	.406	7.998	.068
	p3p4B	.476	5.666	.064
10	UM1M2L	.630	25.714	.088
	p4L	.793	13.737	.069
	UM1W	.564	20.476	.080
	m1m2D	.553	11.221	.065
	m1m2B	.643	7.350	.059
	UP4W	.716	13.983	.069
	p1m3L	.458	11.253	.065
	p3p4D	.398	8.704	.061
	p3p4B	.472	5.823	.057
	p1p4L	.614	4.035	.054
11	UM1M2L	.614	26.303	.077
	p4L	.755	10.904	.056
	UM1W	.520	24.327	.074
	m1m2D	.551	10.854	.056
	m1m2B	.632	7.901	.052
	UP4W	.695	14.877	.061
	p1m3L	.453	11.515	.057
	p3p4D	.386	9.735	.054
	p3p4B	.470	4.511	.047
	p1p4L	.596	4.897	.048
	m1L	.684	4.734	.047

Table 5.113. Measurements selected by the stepwise method in 11 steps, shown with their tolerance, F to remove value and Wilks' Lambda for each step.

From the 11 steps and selected measurements, 3 discriminant functions were created. Table 5.114 shows the functions and their calculated eigenvalues.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	3.525[a]	53.6	53.6	.883
2	2.505[a]	38.1	91.7	.845
3	.543[a]	8.3	100.0	.593

Table 5.114. Eigenvalues of the discriminant functions created by analysis for temporal analysis. The first 3 canonical discriminant functions were used in the analysis.

100% of the variance is explained by the 3 functions. Function 1 accounts for the most variation (53.6%), and combined with function 2, explain a significant proportion of the data (91.7%). The canonical correlations shown represent the multiple correlations between the predictive measurements and the discriminant function.

The significance of the 3 discriminant functions was assessed by Chi-square tests, indicating how well each function separates the cases (each measurement value) into the age groups. The results are shown in Table 5.115.

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 3	.041	302.165	33	.0001
2 through 3	.185	159.509	20	.0001
3	.648	40.977	9	.0001

Table 5.115. Test of functions. Wilks' Lambda and Chi-square analysis of discriminant functions. Significance indicated by $p<0.05$.

Functions 1 through 3 have the greatest discriminatory ability (indicated by small Wilks' Lambda). The Chi-square test found all functions as significant ($p<0.05$). The proportion of variability not explained by the functions 1-3 is 4.1%.

The results from the structure matrix are shown in Table 5.116, indicating the correlation of each measurement with each function.

	Function		
	1	2	3
p4L	**.381***	-.191	-.163
m1m2B	**.277***	.192	.242
UP4W	**-.272***	.207	**-.270**
m1W[a]	.259*	.037	-.129
m1Ltrig[a]	.257*	.168	-.040
UP4L[a]	.165*	.145	.095
p4W[a]	.162*	-.026	-.106
m2W[a]	-.077*	.043	-.024
p1p4L	.067*	-.038	.042
UM1M2L	-.076	**.581***	-.115
m1m2D	-.085	**.514***	.199
UM1L[a]	-.066	.329*	.064
p3p4B	.215	**.310***	.219
UM2W[a]	-.093	.216*	.215
m1L	.200	.210*	-.032
UM1W	**-.301**	.241	**.459***
p1m3L	.126	.101	**.438***
p2m3L[a]	.100	-.019	.295*
p3p4D	-.048	.192	.212*
m2L[a]	-.098	.056	.176*
UP3L[a]	-.099	-.124	.166*
m1Ltal[a]	.094	.110	.124*
p2p4L[a]	.053	-.029	.068*

Table 5.116. The structure matrix showing the pooled within-groups correlations between the discriminating variables and standardised canonical discriminant functions. Correlations of <0.25 ignored due to low correlation. *largest absolute correlation between each variable and any discriminant function. [a] indicates measurements that have not been selected by the stepwise DFA.

As the structure matrix is unaffected by co-linearity, the potentially inflated importance of any linearly correlated measurements has been rectified. For function 1 p4L, M1W, m1m2B and P4W are the most highly correlated measurements. For function 2, M1M2L, m1mD and p3p4B are highly correlated. For function 3, although of least importance, M1W, p1m3L and P4W are highly correlated.

The group centroids for each age group can also be used in describing the separation between each age group, shown in Table 5.117.

	Function		
Age	**1**	**2**	**3**
1	-1.254	1.496	.035
3	-.467	-2.009	1.121
5a	2.796	.083	-.254
7	-2.061	-2.664	-1.631

Table 5.117. Functions at group centroids. Unstandardised canonical discriminant functions evaluated at group means.

The group centroids describe each age group in terms of the means of the function-correlated measurements. Cases with scores near the centroid of each group are predicted as belonging to that group.

Figure 5.79 illustrates the individual canonical scores and group centroids for discriminant functions 1 and 2.

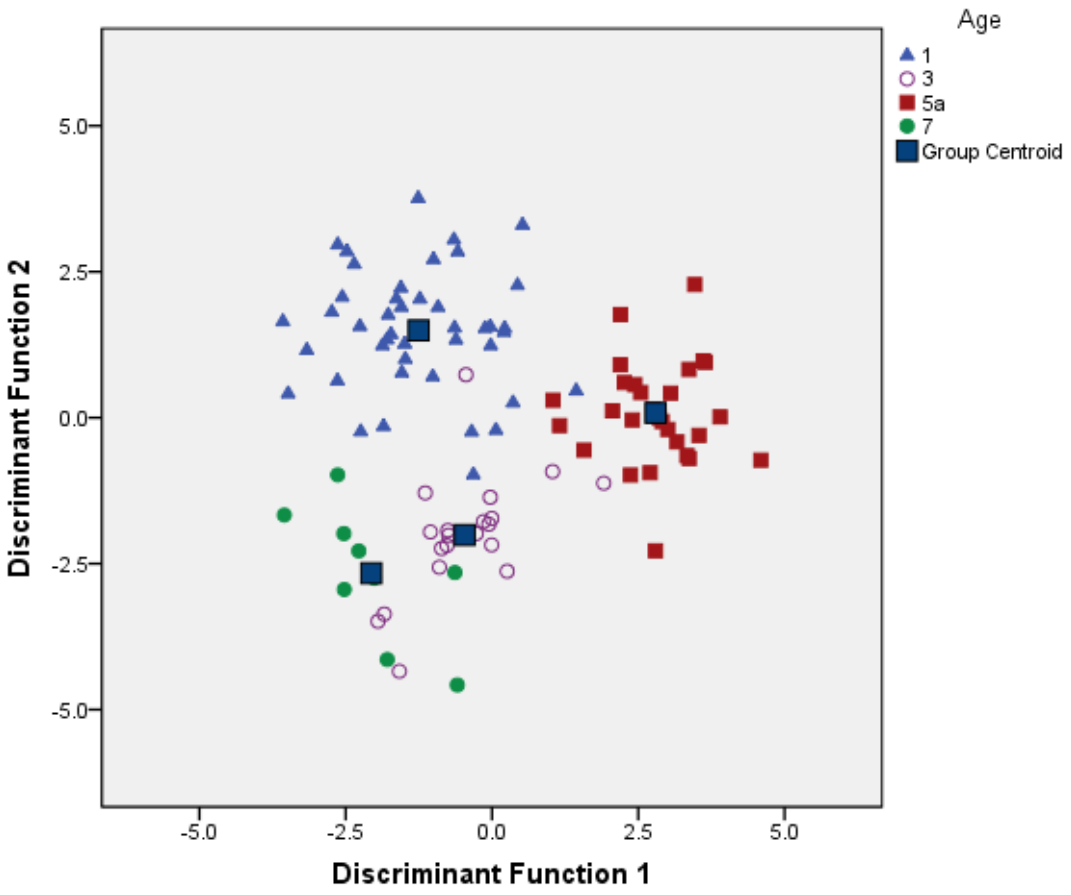


Figure 5.79. Plot of individual canonical scores and group centroids on the first and second discriminant functions from the discriminant analysis of dietary measurements for *C. lupus* temporal groups (MIS 1, 3, 5a and 7).

Function 1 explains 53.6% of the variation, with p4L, m1m2B and M1W, P4W as the most correlated measurements (Table 5.116). Function 1 separates MIS 1, 3 and 7 from MIS 5a. MIS 7 is most separated from MIS 5a, as well as being separated from MIS 1 and 3. The analysis indicates that MIS 5a is characterised with longer p4L and broader m1m2B, with narrower M1W and P4W than the other age groups.

Function 2 explains 38.1% of the variation, with M1M2L, m1m2D and p3p4B as the most correlated measurements (Table 5.116). Function 2 separates MIS 1 and MIS 3 and 7. MIS 5a plots between the age groups. The analysis indicates that MIS 1, and to some extent MIS 5a, has longer M1M2L, deeper m1m2D and broader p3p4B than both MIS 3 and 7.

Function 3 (not illustrated) only explains 8% of the variance, with M1W, p1m3L and P4W the most highly correlated measurements (Table 5.116). This function separated MIS 3 and 7, with MIS 1 and 5a grouped similarly between the age groups, and MIS 3 as having wider M1W, longer p1m3L and narrower P4W than MIS 7.

Based on the 3 discriminant functions, the variation in the discriminant analysis model can be summarised by Table 5.118.

			Predicted Group Membership				
		Age	1	3	5a	7	Total
Original	**Count**	**1**	41	1	1	0	43
		3	1	17	1	1	20
		5a	0	0	30	0	30
		7	0	0	0	10	10
	%	**1**	95.3	2.3	2.3	.0	100.0
		3	5.0	85.0	5.0	5.0	100.0
		5a	.0	.0	100.0	.0	100.0
		7	.0	.0	.0	100.0	100.0
Cross-validated[a]	**Count**	**1**	40	1	2	0	43
		3	1	16	2	1	20
		5a	1	0	29	0	30
		7	0	1	0	9	10
	%	**1**	93.0	2.3	4.7	.0	100.0
		3	5.0	80.0	10.0	5.0	100.0
		5a	3.3	.0	96.7	.0	100.0
		7	.0	10.0	.0	90.0	100.0

Table 5.118. Classification of results based on the stepwise selected measurements and created discriminant functions, for the temporal age groups (MIS 1, 3, 5a and 7) of British C. *lupus*. [a] Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case.

Based on the original dataset, the discriminant functions classify 41 out of 43 (95.3%) cases correctly for MIS 1, with one case predicted as belonging to MIS 3 and the other to MIS 5a. For MIS 3, 17 out of 20 (85%) were correctly classified, with cases wrongly classified into all age groups. For MIS 5a, 30 out of 30 (100%) were correctly classified. For MIS 7, 10 out of 10 (100%) were also correctly classified. The stepwise discriminant model correctly classified 95.1% of cases into their age groups, however, as this is based on the cases themselves, it may be an over-optimistic result.

To correct this, cross-validation was used, whereby each case is classified while leaving it out from analysis. This provides a more honest representation of model power. Based on cross-validation for MIS 1 93% of cross validated cases were correctly classified, with MIS 3 80%, MIS 5a 96.7%, and MIS 7 90%. Thus the cross-validated model correctly classified 91.3% of cases.

5.3.6.2. Stepwise Discriminant Function Analysis: species groups

Stepwise DFA was also performed on the main species groups of *C. lupus*, *C. mosbachensis*, *C. etruscus* and *C. arnensis* to assess the differences in the dietary measurements between these species. The modern Swedish *C. lupus* dataset was combined with Pleistocene *C. lupus*.

Measurements containing low numbers of individuals were removed (p1m3L, p2m3L, DentaryL, C1M2L, P1M2L, P1P4L), as well as m1L and P4L, which are reflective of body mass.

Following the same protocol as the temporal stepwise DFA shown previously, tests of equality of group means using Wilks' Lambda and ANOVA (F) to test the mean differences were used to assess predictive ability of the data. The results are shown in Table 5.119.

	Wilks' Lambda	F	df1	df2	Sig.
m1W	.219	206.232	3	173	.0001
m1Ltrig	.197	234.445	3	173	.0001
m1Ltal	.600	38.377	3	173	.0001
p4L	.385	92.013	3	173	.0001
p4W	.296	136.893	3	173	.0001
m2L	.564	44.511	3	173	.0001
m2W	.429	76.681	3	173	.0001
p1p4L	.301	134.087	3	173	.0001
p2p4L	.383	92.971	3	173	.0001
p3p4D	.175	271.903	3	173	.0001
p3p4B	.235	187.740	3	173	.0001
m1m2D	.174	272.905	3	173	.0001
m1m2B	.266	159.022	3	173	.0001
UP3L	.242	180.350	3	173	.0001
UP4W	.193	240.590	3	173	.0001
UM1L	.276	151.056	3	173	.0001
UM1W	.301	134.216	3	173	.0001
UM2W	.279	149.299	3	173	.0001
UM1M2L	.270	155.893	3	173	.0001

Table 5.119. Results from Wilks' Lambda and tests of equality of group means using ANOVA. Species DFA of *C. lupus*, *C. mosbachensis, C. etruscus* and *C. arnensis*.

All measurements effectively contribute to the DFA by their relatively low Wilks' Lambda values. The F test found all measurements as significant (p<0.05) in their group differences, also indicating strong predictive abilities.

Correlations were assessed between the measurements. The highest correlated measurements were m1Ltrig and m1W (0.735).

The log determinants are shown in Table 5.120.

Species	Rank	Log Determinant
1	11	2.257
2	11	-7.420
3	11	-11.911
4	.[a]	.[b]
Pooled within-groups	11	1.250

Table 5.120. Log determinants. The ranks and natural logarithms of determinants are those of the group covariance matrices. The ranks and natural logarithms of determinants are those of the group covariance matrices, a. Rank < 11, b. The DFA found too few cases for it to be non-singular. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*.

The log determinants for *C. lupus* (1), *C. mosbachensis* (2) and *C. etruscus* (3) were dissimilar. *C. arnensis* (4) was identified as singular. The difference between the species suggests differing covariance matrices, and thus relates to sample size differences.

Box's M was significant (Box's M = 426.029, $F_{(132,\ 5899.640)}$ = 2.513, p=0.0001), also indicating the covariance matrices differ. In similarity to the temporal DFA of *C. lupus*, the significant Box's M may be due to low sample numbers, and unequal group sample sizes, which will be a caveat in the analysis.

The result of the stepwise selection method is shown in Table 5.121, based on measurements that lowered the Wilks' Lambda being entered.

Step	Entered	Wilks' Lambda											
						Exact F				Approximate F			
		Statistic	df1	df2	df3	Statistic	df1	df2	Sig.	Statistic	df1	df2	Sig.
1	m1m2D	.174	1	3	173.000	272.905	3	173.000	.0001				
2	m1Ltrig	.081	2	3	173.000	144.409	6	344.000	.0001				
3	UP4W	.051	3	3	173.000					111.226	9	416.320	.0001
4	p1p4L	.035	4	3	173.000					95.657	12	450.069	.0001
5	p4W	.029	5	3	173.000					80.791	15	466.936	.0001
6	UM1L	.024	6	3	173.000					72.313	18	475.661	.0001
7	m1m2B	.021	7	3	173.000					65.212	21	480.084	.0001
8	UM1M2L	.018	8	3	173.000					60.083	24	482.052	.0001
9	p3p4D	.016	9	3	173.000					55.594	27	482.527	.0001
10	p2p4L	.015	10	3	173.000					51.388	30	482.048	.0001
11	UM2W	.014	11	3	173.000					47.917	33	480.932	.0001

Table 5.121. Results from stepwise selection. Measurements shown were entered by the model in 11 steps. At each step, the variable that minimises the overall Wilks' Lambda is entered. a. Maximum number of steps is 38, b. Minimum partial F to enter is 3.84, c. Maximum partial F to remove is 2.71, d. F level, tolerance, or VIN insufficient for further computation.

In total 11 steps were taken, selecting m1m2D, m1Ltrig, P4W, p1p4L, p4W, M1L, m1m2B, M1M2L, p3p4D, p2p4L, M2W, based on their ability of lowering Wilks' Lambda.

The number of steps and the measurements selected are also shown in Table 5.122, with their tolerance, F to remove value and Wilks' Lambda value indicated. A variable with low tolerance contributes little to the model, and may be of concern if <0.40. As Table 5.122 shows, all measurements selected are >0.40 in tolerance.

Step		Tolerance	F to Remove	Wilks' Lambda
1	m1m2D	1.000	272.905	
2	m1m2D	.957	82.807	.197
	m1Ltrig	.957	66.502	.174
3	m1m2D	.957	41.186	.087
	m1Ltrig	.915	53.931	.099
	UP4W	.955	33.775	.081
4	m1m2D	.957	29.557	.053
	m1Ltrig	.902	51.397	.067
	UP4W	.948	32.718	.055
	p1p4L	.980	25.439	.051
5	m1m2D	.917	32.968	.046
	m1Ltrig	.900	33.535	.047
	UP4W	.944	28.904	.044
	p1p4L	.980	22.195	.041
	p4W	.943	11.120	.035
6	m1m2D	.912	27.765	.036
	m1Ltrig	.892	33.444	.038
	UP4W	.932	22.958	.034
	p1p4L	.972	14.509	.030
	p4W	.908	13.368	.030
	UM1L	.909	12.107	.029
7	m1m2D	.858	15.514	.027
	m1Ltrig	.868	35.153	.034
	UP4W	.905	25.088	.030
	p1p4L	.946	12.941	.026
	p4W	.908	11.629	.025
	UM1L	.903	12.484	.025
	m1m2B	.850	8.658	.024
8	m1m2D	.819	14.251	.023
	m1Ltrig	.864	31.331	.028
	UP4W	.878	20.953	.025
	p1p4L	.941	13.128	.022
	p4W	.905	11.728	.022
	UM1L	.898	9.370	.021
	m1m2B	.814	9.872	.021
	UM1M2L	.859	8.415	.021
9	m1m2D	.784	8.192	.019
	m1Ltrig	.861	28.942	.025
	UP4W	.878	18.610	.022
	p1p4L	.936	12.352	.020
	p4W	.899	11.987	.020

	UM1L	.897	8.795	.019
	m1m2B	.813	8.345	.019
	UM1M2L	.859	8.353	.019
	p3p4D	.904	6.646	.018
10	m1m2D	.783	7.938	.017
	m1Ltrig	.861	27.671	.022
	UP4W	.858	19.004	.020
	p1p4L	.935	11.891	.018
	p4W	.898	11.021	.018
	UM1L	.890	6.668	.017
	m1m2B	.812	7.908	.017
	UM1M2L	.813	10.441	.018
	p3p4D	.845	5.538	.016
	p2p4L	.834	4.700	.016
11	m1m2D	.780	7.958	.016
	m1Ltrig	.856	27.353	.021
	UP4W	.816	11.968	.017
	p1p4L	.927	12.025	.017
	p4W	.897	9.801	.016
	UM1L	.880	6.191	.015
	m1m2B	.806	8.254	.016
	UM1M2L	.811	10.292	.016
	p3p4D	.844	4.812	.015
	p2p4L	.831	4.792	.015
	UM2W	.868	4.413	.015

Table 5.122. Measurements entered into the DFA in the 11 steps, showing their tolerance, F to remove value and Wilks' Lambda for each step.

Based on the 11 steps and their selected measurements, 3 discriminant functions were created by the DFA. Table 5.123 shows the functions and calculated eigenvalues.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	39.708[a]	98.2	98.2	.988
2	.562[a]	1.4	99.6	.600
3	.147[a]	.4	100.0	.358

Table 5.123. Eigenvalues of the discriminant functions created by analysis for species analysis. The first 3 canonical discriminant functions were used in the analysis.

The 3 functions explain 100% of the variance. Function 1 accounts for the most variation (98.2%). Both function 2 and 3 explain less variation (1.4% and 0.4%). When combined with function 2, almost all data is explained (99.6%). The canonical correlations shown represent the multiple correlations between the predictive measurements and the discriminant function.

The significance of the discriminant functions was assessed by Wilks' Lambda and Chi-square tests, indicating how well each function separated the cases into the species groups. Table 5.124 shows the results.

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 3	.014	722.704	33	.0001
2 through 3	.558	98.172	20	.0001
3	.872	23.050	9	.006

Table 5.124. Wilks' Lambda and Chi-square analysis of discriminant functions. Significance indicated by $p<0.05$.

Functions 1 through 3 have the greatest discriminatory ability (indicated by small Wilks' Lambda). The Chi-square test found all functions as significant ($p<0.05$). The proportion of variability not explained by the functions is 1-3, 1.4%.

The structure matrix indicating the correlation of each measurement is shown in Table 5.125.

	Function		
	1	2	3
p3p4D	**.344***	-.158	**-.307**
UP4W	**.323***	-.218	**.321**
m1Ltrig	**.319***	-.187	.172
m1m2B	**.263***	-.119	.032
UM2W	**.254***	-.216	-.003
m1W[a]	.249*	-.021	.115
p4W	.244*	.018	.029
m2W[a]	.192*	-.080	-.030
UP3L[a]	.145*	-.023	.049
m2L[a]	.124*	.028	.068
p4L[a]	.121*	.045	-.058
m1Ltal[a]	-.103*	.036	.080
p1p4L	.232	**.543***	-.456
UM1L	.251	**.455***	.038
p2p4L	.199	.251*	-.194
UM1W[a]	.015	.044*	.003
m1m2D	**.344**	-.111	**-.503***
UM1M2L	**.257**	**.305**	**.463***
p3p4B[a]	.072	-.119	-.155*

Table 5.125. Structure matrix showing the pooled within-groups correlations between the discriminating variables and standardised canonical discriminant functions. Correlations of <0.25 ignored due to low correlation. *Largest absolute correlation between each variable and any discriminant function, [a] indicates measurements that have not been selected in the analysis.

For function 1 p3p4D, m1m2D, P4W, m1Ltrig, m1m2B, M2W, M1L were the most highly correlated measurements. For function 2, p1p4L, M1L, p2p4L and M1M2L were highly correlated. For function 3, although of least importance, m1m2D, M1M2L, p1p4L, p3p4D, and P4W were highly correlated.

The group centroids for each age group also highlight the separation between each species group centroid, shown in Table 5.126.

Species	Function		
	1	2	3
1	4.123	-.088	-.039
2	-9.372	-.804	.488
3	-5.411	2.199	.267
4	-12.779	-.113	-1.247

Table 5.126. Functions at group centroids. Unstandardised canonical discriminant functions evaluated at group means. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*.

The group centroids describe each species group in terms of the overall means of the measurements. Cases with scores near the centroid of each group are predicted as belonging to that group. Figure 5.80 illustrates the individual canonical scores and group centroids for functions 1 and 2.

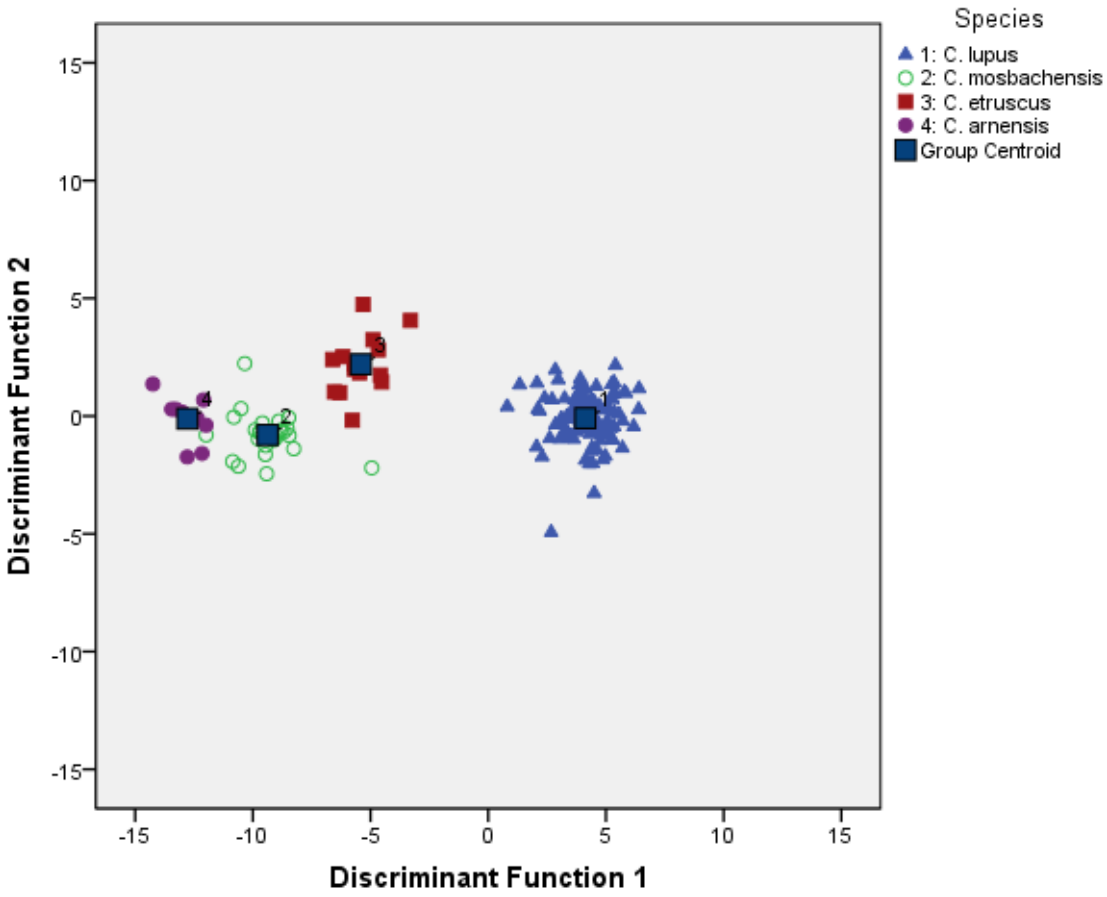


Figure 5.80. Plot of individual canonical scores and group centroids on the first and second discriminant functions from the discriminant analysis of dietary measurements for species groups.

Function 1 explained 98.2% of the variation, with p3p4D, m1m2D, P4W, m1Ltrig, m1m2B, M2W and M1L as the most correlated measurements. Function 1 clearly separated all

species, with *C. lupus* differentiated by deeper jaws at the premolars and molars, as well as broader jaws at the molars, longer carnassial blades and wider upper carnassials, wider M2 and longer buccal length of M1. *C. etruscus, C. mosbachensis* and *C. arnensis* are grouped separately, with *C. etruscus* having elongated measurements in comparison to *C. arnensis*, and *C. mosbachensis* plotted between these species.

Function 2 explained only 1.4% of the variation, with p1p4L, M1L, p2p4L and M1M2L as the most correlated measurements. Function 2 created less separation, with *C. etruscus* most separated from *C. mosbachensis*. *C. etruscus* was characterised by having a longer premolar row and buccal length of the upper molar complex, combined with a longer M1 buccal length than in the other species.

Function 3 (not illustrated) only explains 0.4% of the variance, with m1m2D, M1M2L, p1p4L, p3p4D, and P4W the most highly correlated measurements. This function separated *C. arnensis* from the other canids as having narrower jaws, shorter premolar row and narrower upper carnassial.

Using the 3 discriminant functions created by the DFA, the variation in the discriminant analysis model can be summarised by Table 5.127.

			Predicted Group Membership				
		Species	1	2	3	4	Total
Original	**Count**	**1**	121	0	0	0	121
		2	0	27	1	1	29
		3	0	0	16	0	16
		4	0	0	0	11	11
	%	**1**	100.0	.0	.0	.0	100.0
		2	.0	93.1	3.4	3.4	100.0
		3	.0	.0	100.0	.0	100.0
		4	.0	.0	.0	100.0	100.0
Cross-validated[a]	**Count**	**1**	121	0	0	0	121
		2	0	27	1	1	29
		3	0	0	16	0	16
		4	0	0	0	11	11
	%	**1**	100.0	.0	.0	.0	100.0
		2	.0	93.1	3.4	3.4	100.0
		3	.0	.0	100.0	.0	100.0
		4	.0	.0	.0	100.0	100.0

Table 5.127. Classification of results based on the stepwise selected measurements and created discriminant functions. [a] Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*.

Based on the original data, 100% of cases were correctly classified for *C. lupus, C. etruscus* and *C. arnensis*. However, 93.1% were correctly classified for *C. mosbachensis*, with 3.4% wrongly classified in both *C. etruscus* and *C. arnensis*. The stepwise discriminant model therefore correctly classified 98.9% of cases into their species groups, however, as this is based on the cases themselves to create the model, it may be an over-optimistic result.

Cross-validation was used to providing a more honest representation of model power. Again 100% of cases were correctly classified as *C. lupus, C. etruscus* and *C. arnensis*, with 93.1% for *C. mosbachensis*, of which 3.4% were classified wrongly as *C. etruscus* and *C. arnensis*. Thus the cross-validated model correctly classified 98.9% of cases.

5.3.6.2.1. The effect of size: using Mosimann shape variables in the species groups DFA

There is a possibility that the stepwise DFA for the species groups is discriminating body size rather than dietary differences. Although the stepwise method selects measurements that are the best predictors of group membership, these measurements may nonetheless be influenced by body size. To reduce the effect of size, Mosimann shape variables were calculated and used instead of the previously raw measurements. The same process for the stepwise DFA was carried out as above. Table 5.128 shows the results of the tests of equality of group means.

	Wilks' Lambda	F	df1	df2	Sig.
GMm1W	.316	56.181	3	78	.0001
GMm1Ltrig	.289	64.041	3	78	.0001
GMm1Ltal	.765	7.987	3	78	.0001
GMp4L	.473	29.001	3	78	.0001
GMp4W	.409	37.523	3	78	.0001
GMm2L	.684	12.022	3	78	.0001
GMm2W	.704	10.924	3	78	.0001
GMp1p4L	.567	19.888	3	78	.0001
GMp2p4L	.679	12.307	3	78	.0001
GMp3p4D	.299	60.822	3	78	.0001
GMp3p4B	.480	28.170	3	78	.0001
GMm1m2D	.279	67.179	3	78	.0001
GMm1m2B	.491	26.940	3	78	.0001
GMUP3L	.490	27.075	3	78	.0001
GMUP4W	.406	38.042	3	78	.0001
GMUM1L	.465	29.881	3	78	.0001
GMUM1W	.475	28.742	3	78	.0001
GMUM2W	.505	25.495	3	78	.0001
GMUM1M2L	.508	25.185	3	78	.0001

Table 5.128. Results from Wilks' Lambda and tests of equality of group means using ANOVA. Species DFA of *C. lupus*, *C. mosbachensis, C. etruscus* and *C. arnensis* using Mosimann shape variables.

The Wilks' Lambda values have slightly increased in comparison to the original species DFA (Table 5.119) by using the shape variables, indicating they contribute relatively less to the DFA. Nonetheless, the F test found all shape variables as significant (p<0.05) in their group differences, indicating strong predictive abilities.

Correlations were again assessed between the shape variables. The highest correlated shape variables were m1Ltrig and m1W (0.826) and p4L and p4W (0.529).

The log determinants are shown in Table 5.129.

Species	Rank	Log Determinant
1	6	-32.298
2	6	-34.891
3	.[a]	.[b]
4	.[c]	.[b]
Pooled within-groups	6	-32.343

Table 5.129. Log determinants for the species groups. The ranks and natural logarithms of determinants are those of the group covariance matrices. The ranks and natural logarithms of determinants are those of the group covariance matrices. a. Rank < 4, b. The DFA found too few cases for it to be non-singular. c. Rank < 3. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*.

The log determinants for *C. lupus* (1) and *C. mosbachensis* (2) are similar. Both *C. etruscus* (3) and *C. arnensis* (4) were found to be singular due to low cases. The differences suggest differing covariance matrices, likely relating to the sample size differences.

Box's M was non-significant (Box's M = 43.876, $F_{(21,\ 537.128)}$ = 1.369, p=0.127), indicating similar covariance matrices, in contrast to the original species DFA and temporal DFA.

The result from the stepwise selection method is shown in Table 5.130, based on how each shape variable lowers the Wilks' Lambda.

Step	Entered	Wilks' Lambda											
						Exact F				Approximate F			
		Statistic	df1	df2	df3	Statistic	df1	df2	Sig.	Statistic	df1	df2	Sig.
1	GMm1m2D	.279	1	3	78.000	67.179	3	78.000	.0001				
2	GMm1Ltrig	.155	2	3	78.000	39.519	6	154.000	.0001				
3	GMUP4W	.107	3	3	78.000					30.905	9	185.115	.0001
4	GMp4W	.082	4	3	78.000					25.980	12	198.723	.0001
5	GMp1p4L	.070	5	3	78.000					22.069	15	204.683	.0001
6	GMUM1W	.060	6	3	78.000					19.644	18	206.960	.0001

Table 5.130. Results from stepwise selection. Shape variables shown were entered by the model in 6 steps. At each step, the variable that minimises the overall Wilks' Lambda is entered. a. Maximum number of steps is 38, b. Minimum partial F to enter is 3.84, c. Maximum partial F to remove is 2.71, d. F level, tolerance, or VIN insufficient for further computation.

As shown by Table 5.130, in 6 steps the following shape variables were selected; m1m2D, m1Ltrig, P4W, p4W, p1p4L and M1W, based on their ability to lower the overall Wilks' Lambda.

The number of steps and the shape variables selected is also shown in Table 5.131, as well as indicating their tolerance, F to remove value and Wilks' Lambda. A variable with low tolerance contributes little to the model, and may be of concern if <0.40. As Table 5.131 shows, all shape variables selected are >0.40 in tolerance.

Step		Tolerance	F to Remove	Wilks' Lambda
1	GMm1m2D	1.000	67.179	
2	GMm1m2D	.996	22.137	.289
	GMm1Ltrig	.996	20.527	.279
3	GMm1m2D	.995	11.649	.157
	GMm1Ltrig	.921	22.455	.202
	GMUP4W	.923	11.285	.155
4	GMm1m2D	.970	11.728	.121
	GMm1Ltrig	.920	15.825	.135
	GMUP4W	.918	9.329	.113
	GMp4W	.969	7.541	.107
5	GMm1m2D	.963	11.565	.103
	GMm1Ltrig	.918	14.470	.111
	GMUP4W	.914	9.038	.096
	GMp4W	.966	5.981	.087
	GMp1p4L	.982	4.279	.082
6	GMm1m2D	.963	9.539	.083
	GMm1Ltrig	.918	11.769	.089
	GMUP4W	.913	8.017	.079
	GMp4W	.960	5.818	.074
	GMp1p4L	.937	5.477	.073
	GMUM1W	.945	4.284	.070

Table 5.131. Selected variables in the analysis. Shape variables with their tolerance, F to remove value and Wilks' Lambda for each step.

From the 6 steps and selected shape variables, 3 discriminant functions were created.

Table 5.132 shows the functions and calculated eigenvalues.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	13.765[a]	99.1	99.1	.966
2	.105[a]	.8	99.8	.308
3	.026[a]	.2	100.0	.161

Table 5.132. Eigenvalues of the discriminant functions created by analysis for species analysis. The first 3 canonical discriminant functions were used in the analysis.

The 3 functions created by the analysis explain 100% of the variance. Function 1 accounts for the most variation (99.1%). Both function 2 and 3 explain less variation (0.8% and 0.2%). When combined with function 2, almost all data is explained (99.8%). The canonical

correlations shown represent the multiple correlations between the predictive shape variables and the discriminant function.

The significance of the functions was further assessed by Wilks' Lambda and Chi-square tests, indicating how well each function separates the cases into species groups. Table 5.133 shows the results.

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 3	.060	214.187	18	.0001
2 through 3	.882	9.576	10	.478
3	.974	1.985	4	.739

Table 5.133. Wilks' Lambda and Chi-square analysis of discriminant functions for the species DFA using the Mosimann shape variables. Significance indicated by $p<0.05$.

Functions 1 through 3 have the greatest discriminatory ability (indicated by small Wilks' Lambda). The Chi-square test found functions 1-3 as significant ($p<0.05$). The proportion of variability not explained by the functions 1-3 6.0%.

The structure matrix showing the correlations of each shape variable with the functions is shown in Table 5.134.

	Function		
	1	2	3
GMm1Ltrig	**.422***	-.235	.222
GMm1W[a]	.420*	-.093	.155
GMm2L[a]	.251*	.054	.090
GMm2W[a]	.236*	-.023	.147
GMp3p4D[a]	.183*	-.124	-.009
GMUM1M2L[a]	.165*	-.077	-.068
GMm1Ltal[a]	-.111*	.063	.059
GMUM1L[a]	.103*	-.021	.047
GMp1p4L	.226	**.765***	-.074
GMUM1W	**.282**	**.323***	-.035
GMm1m2D	**.431**	**-.322**	**-.823***
GMUP4W	**.325**	-.143	**.355***
GMp4W	**.323**	-.030	**.344***
GMm1m2B[a]	.005	.133	-.237*
GMp4L[a]	.161	.050	.210*
GMUP3L[a]	.104	.018	.191*
GMUM2W[a]	.044	-.118	.190*
GMp2p4L[a]	-.035	-.042	-.122*
GMp3p4B[a]	-.033	-.096	-.103*

Table 5.134. Structure matrix showing the pooled within-groups correlations between the discriminating variables and standardised canonical discriminant functions. Correlations of <0.25 ignored due to low correlation. *Largest absolute correlation between each variable and any discriminant function, [a] indicates the shape variables that have not been selected in the analysis.

For function 1, the shape variables of m1Ltrig, m1m2D, P4W, p4W and M1W are the most highly correlated measurements. For function 2, the shape variables of p1p4L, M1W and m1m2D are highly correlated. For function 3, although of least importance, m1m2D, P4W and p4W shape variables are highly correlated.

The group centroids for each species group can also be used in describing the between-group separation, shown in Table 5.135.

	Function		
Species	**1**	**2**	**3**
1	1.672	-.019	-.013
2	-7.862	-.558	.189
3	-4.755	1.148	.340
4	-10.025	.371	-.659

Table 5.135. Functions at group centroids. Unstandardised canonical discriminant functions evaluated at group means. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*.

The group centroids describe each group in terms of the overall means of the measurements. Figure 5.81 illustrates the individual canonical scores and group centroids for discriminant functions 1 and 2.

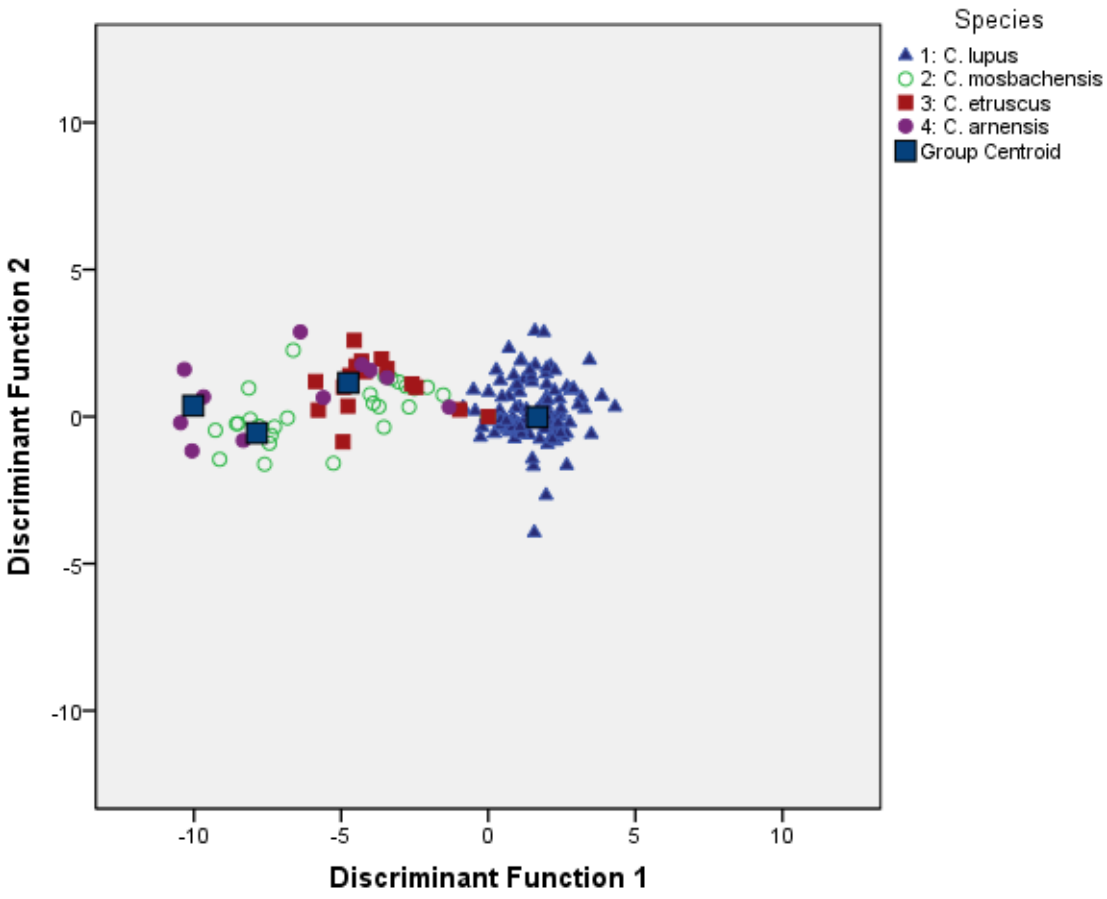


Figure 5.81. Plot of individual canonical scores and group centroids on the first and second discriminant functions from the discriminant analysis of Mosimann shape variables for species groups.

Function 1 explains 99.1% of the variation, with m1Ltrig, m1m2D, P4W, p4W and M1W as the most correlated shape variables. Function 1 separated all species, although with some overlap. *C. lupus* is separated by having longer carnassial blades, with wider upper carnassials, deeper jaws at the molars, wider p4 and M1. *C. etruscus, C. mosbachensis* and *C. arnensis* are grouped separately, with *C. etruscus* having elongated measurements in comparison to *C. arnensis*, and *C. mosbachensis* lying in-between.

Function 2 explains 0.8% of the variation, with p1p4L, M1W and m1m2D as the most correlated shape variables. Function 2 created much less separation, with *C. etruscus* most separated from *C. mosbachensis*. *C. etruscus* is characterised as having a longer premolar row and wider M1, with narrower jaws at the molars, than the other species.

Function 3 (not illustrated) only explains 0.4% of the variance, with m1m2D, P4W and p4W the most highly correlated shape variables. This function slightly separates *C. arnensis* from the other canids by its slightly wider jaw at the molars, as well as its narrower P4 and p4.

Using the 3 discriminant functions, the variation in the discriminant analysis model can be summarised by Table 5.136.

			Predicted Group Membership				
		Species	1	2	3	4	Total
Original	**Count**	**1**	121	0	0	0	121
		2	4	13	12	0	29
		3	2	0	14	0	16
		4	1	1	5	4	11
	%	**1**	100.0	.0	.0	.0	100.0
		2	13.8	44.8	41.4	.0	100.0
		3	12.5	.0	87.5	.0	100.0
		4	9.1	9.1	45.5	36.4	100.0
Cross-validated[a]	**Count**	**1**	121	0	0	0	121
		2	5	10	12	2	29
		3	3	3	10	0	16
		4	0	2	5	4	11
	%	**1**	100.0	.0	.0	.0	100.0
		2	17.2	34.5	41.4	6.9	100.0
		3	18.8	18.8	62.5	.0	100.0
		4	.0	18.2	45.5	36.4	100.0

Table 5.136. Classification of results based on stepwise selected shape variables and created discriminant functions. [a] Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*.

Based on the original data, 100% of cases were classified correctly for *C. lupus,* 44.8% for *C. mosbachensis*, with wrongly classified cases as *C. lupus* and *C. etruscus*, 87.5% for *C. etruscus*, with wrongly classified cases as *C. lupus* only, and 36.4% for *C. arnensis*, which had wrongly classified cases in all species. The stepwise discriminant model therefore correctly classified 85.9% of cases to their species groups, however, as this is based on the cases themselves to create the model, it may be an over-optimistic result.

As done previously, cross-validation was used, whereby 100% of cases were again correctly classified for *C. lupus,* with 34.5% correctly classified for *C. mosbachensis* and wrongly classified cases again in all species. For *C. etruscus*, 62.5% were correctly classified with wrongly classified cases in both *C. lupus* and *C. mosbachensis*. For *C. arnensis*, 36.4% were correctly classified, with wrongly classified cases in *C. mosbachensis* and *C. etruscus*. Thus the cross-validated model correctly classified 81.9% of cases.

Summary

It is interesting that both DFAs recognised similar measurements, both when in linear form, and when a Mosimann shape variable. Both stepwise DFAs also separated the species

similarly on function 1. Hence, even though body size was accounted for by using the Mosimann Shape variables, it seems that the influence of size on the selected measurements/shape variables was minimal. The main difference between both models was in the effectiveness of the discriminant functions in separating the species groups, with the raw measurement DFA classifying 98.9% (cross-validated), and the Mosimann shape variable DFA classifying 81.9% (cross validated).

5.3.6.3. Species differences: Pleistocene and modern canids compared

A further stepwise discriminant analysis was performed on the four main canid species (*C. etruscus*, *C. arnensis, C. mosbachensis* and *C. lupus* [including modern Swedish wolves]), with the addition of other modern canid species such as *C. adustus, C. aureus, C. mesomelas, C. alpinus* and *L. pictus*, to investigate how the Pleistocene species differ from the modern canids.

As no differences were found between using the Mosimann shape variables and the linear measurements, the latter will be used here.

In similarity to all the previous DFA, the predictive ability of the measurements was assessed by tests of equality of group means, involving Wilks' Lambda with ANOVA (F) to test the mean differences. Table 5.137 shows the results.

	Wilks' Lambda	F	df1	df2	Sig.
m1W	.082	437.271	8	312	.0001
m1Ltrig	.057	639.883	8	312	.0001
m1Ltal	.250	116.762	8	312	.0001
p4L	.084	425.947	8	312	.0001
p4W	.098	357.073	8	312	.0001
m2L	.152	217.744	8	312	.0001
m2W	.142	236.069	8	312	.0001
p1p4L	.064	569.903	8	312	.0001
p2p4L	.068	538.760	8	312	.0001
p3p4D	.067	544.196	8	312	.0001
p3p4B	.095	370.235	8	312	.0001
m1m2D	.064	568.451	8	312	.0001
m1m2B	.094	374.457	8	312	.0001
UP3L	.055	666.375	8	312	.0001
UP4W	.068	533.773	8	312	.0001
UM1L	.111	313.816	8	312	.0001
UM1W	.090	392.336	8	312	.0001
UM2W	.084	427.568	8	312	.0001
UM1M2L	.092	384.494	8	312	.0001

Table 5.137. Results from Wilks' Lambda and tests of equality of group means using ANOVA. Species DFA of both Pleistocene and modern canids.

All measurements effectively contribute to the DFA (low Wilks' Lambda values). The F test found all measurements as significant (p<0.05), also indicating strong predictive abilities.

Correlations were assessed between the measurements. The highest correlated measurements were m1Ltrig and m1W (0.642) and p4L and p4W (0.587)

The log determinants are shown in Table 5.138.

Species	Rank	Log Determinant
1	14	-2.121
2	14	-14.102
3	14	-23.504
4	.[a]	.[b]
5	14	-19.377
6	14	-19.142
7	14	-24.021
8	14	-20.551
9	14	-16.773
Pooled within-groups	14	-5.719

Table 5.138. Log determinants. The ranks and natural logarithms of determinants are those of the group covariance matrices. The ranks and natural logarithms of determinants printed are those of the group covariance matrices. a. Rank < 11, b. The DFA found too few cases for it to be non-singular. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*, 5: *C. adustus*, 6: *C. aureus*, 7: *C. mesomelas*, 8: *C. alpinus*, 9: *L. pictus*.

The log determinant for *C. lupus* (1) is the most dissimilar to all other species groups. As previously, *C. arnensis* (4) was considered singular. The difference between the species suggests differing covariance matrices, relating to the sample size differences.

Box's M was significant (Box's M = 2199.980, $F_{(735, 33620.755)}$ = 2.335, p=0.0001), indicating the covariance matrices differ. As with the previous DFAs, the significant Box's M is likely due to low sample numbers, and unequal sample sizes for the age groups, taken as a caveat in the analysis.

The result from the stepwise selection of measurements is shown in Table 5.139.

Step	Entered	Wilks' Lambda											
						Exact F				Approximate F			
		Statistic	df1	df2	df3	Statistic	df1	df2	Sig.	Statistic	df1	df2	Sig.
1	UP3L	.055	1	8	312.000	666.375	8	312.000	.0001				
2	UM2W	.012	2	8	312.000	313.270	16	622.000	.0001				
3	m1m2D	.004	3	8	312.000					207.318	24	899.696	.0001
4	UM1M2L	.002	4	8	312.000					157.061	32	1141.131	.0001
5	m1Ltrig	.001	5	8	312.000					125.876	40	1345.335	.0001
6	p2p4L	.001	6	8	312.000					106.690	48	1514.631	.0001
7	UP4W	.001	7	8	312.000					90.800	56	1653.171	.0001
8	UM1L	.000	8	8	312.000					80.178	64	1765.691	.0001
9	p1p4L	.000	9	8	312.000					71.216	72	1856.739	.0001
10	m2L	.000	10	8	312.000					64.392	80	1930.324	.0001
11	p3p4B	.000	11	8	312.000					58.820	88	1989.806	.0001
12	p4W	.000	12	8	312.000					54.044	96	2037.921	.0001
13	p4L	.000	13	8	312.000					50.470	104	2076.865	.0001
14	m1W	.000	14	8	312.000					47.054	112	2108.385	.0001

Table 5.139. Results from the stepwise selection. Measurements shown were entered by the model in 14 steps. At each step, the variable that minimises the overall Wilks' Lambda is entered. a. Maximum number of steps is 38. b. Minimum partial F to enter is 3.84. c. Maximum partial F to remove is 2.71. d. F level, tolerance, or VIN insufficient for further computation.

In total 14 steps were taken by the DFA to enter the measurements that effectively lowered Wilks' Lambda, including: P3L, M2W, m1m2D, M1M2L, m1Ltrig, p2p4L, P4W, M1L, p1p4L, m2L, p3p4B, p4W, p4L and m1W.

The number of steps taken and measurements selected are also shown in Table 5.140, as well as their tolerance, F to remove value and Wilks' Lambda. A variable with low tolerance contributes little to the model, and may be of concern if <0.40. As Table 5.140 shows, all measurements selected are >0.40 in tolerance.

Step		Tolerance	F to Remove	Wilks' Lambda
1	UP3L	1.000	666.375	
2	UP3L	.935	227.763	.084
	UM2W	.935	137.492	.055
3	UP3L	.935	47.078	.010
	UM2W	.935	127.951	.019
	m1m2D	.999	70.327	.012
4	UP3L	.920	47.679	.004
	UM2W	.886	89.237	.007
	m1m2D	.946	56.551	.005
	UM1M2L	.868	45.618	.004
5	UP3L	.911	24.568	.002
	UM2W	.886	85.859	.004
	m1m2D	.924	37.704	.002
	UM1M2L	.847	46.617	.002
	m1Ltrig	.948	29.096	.002
6	UP3L	.908	15.962	.001
	UM2W	.885	78.197	.002
	m1m2D	.878	38.125	.001
	UM1M2L	.833	47.855	.002
	m1Ltrig	.930	28.497	.001
	p2p4L	.933	23.887	.001
7	UP3L	.885	9.860	.001
	UM2W	.863	80.728	.002
	m1m2D	.876	23.921	.001
	UM1M2L	.786	52.234	.001
	m1Ltrig	.913	26.132	.001
	p2p4L	.928	23.362	.001
	UP4W	.830	13.257	.001
8	UP3L	.859	10.981	.000
	UM2W	.852	76.322	.001
	m1m2D	.874	22.174	.001
	UM1M2L	.759	31.698	.001
	m1Ltrig	.913	25.550	.001
	p2p4L	.907	24.107	.001
	UP4W	.825	13.157	.001
	UM1L	.834	12.956	.001
9	UP3L	.857	9.563	.000
	UM2W	.852	75.993	.001
	m1m2D	.867	21.952	.000

	UM1M2L	.759	30.765	.001
	m1Ltrig	.913	25.422	.001
	p2p4L	.816	9.153	.000
	UP4W	.824	13.127	.000
	UM1L	.827	12.705	.000
	p1p4L	.850	8.396	.000
10	UP3L	.855	9.607	.000
	UM2W	.849	61.151	.001
	m1m2D	.867	21.555	.000
	UM1M2L	.756	23.419	.000
	m1Ltrig	.911	25.277	.000
	p2p4L	.815	9.014	.000
	UP4W	.824	12.681	.000
	UM1L	.818	12.444	.000
	p1p4L	.845	7.823	.000
	m2L	.945	7.714	.000
11	UP3L	.855	9.576	.000
	UM2W	.849	58.224	.001
	m1m2D	.822	12.837	.000
	UM1M2L	.756	23.338	.000
	m1Ltrig	.909	24.137	.000
	p2p4L	.807	9.429	.000
	UP4W	.810	10.003	.000
	UM1L	.818	11.687	.000
	p1p4L	.845	7.799	.000
	m2L	.933	8.122	.000
	p3p4B	.878	6.464	.000
12	UP3L	.848	9.418	.000
	UM2W	.846	58.050	.001
	m1m2D	.812	13.374	.000
	UM1M2L	.756	23.269	.000
	m1Ltrig	.890	18.743	.000
	p2p4L	.801	9.600	.000
	UP4W	.805	8.622	.000
	UM1L	.800	12.526	.000
	p1p4L	.841	7.577	.000
	m2L	.932	8.159	.000
	p3p4B	.878	6.025	.000
	p4W	.910	4.997	.000
13	UP3L	.847	8.693	.000
	UM2W	.846	57.035	.000
	m1m2D	.812	12.755	.000
	UM1M2L	.751	22.332	.000
	m1Ltrig	.882	18.955	.000
	p2p4L	.801	8.696	.000
	UP4W	.801	8.647	.000
	UM1L	.796	12.173	.000
	p1p4L	.819	4.776	.000
	m2L	.921	8.268	.000
	p3p4B	.868	6.459	.000
	p4W	.621	7.202	.000
	p4L	.606	6.224	.000

14	UP3L	.846	8.151	.000
	UM2W	.846	54.937	.000
	m1m2D	.812	12.711	.000
	UM1M2L	.748	22.077	.000
	m1Ltrig	.548	12.614	.000
	p2p4L	.787	9.363	.000
	UP4W	.797	8.725	.000
	UM1L	.793	12.234	.000
	p1p4L	.812	5.046	.000
	m2L	.896	8.817	.000
	p3p4B	.867	6.425	.000
	p4W	.616	6.914	.000
	p4L	.606	6.083	.000
	m1W	.522	4.089	.000

Table 5.140. Variables in the analysis. Measurements with their tolerance, F to remove value and Wilks' Lambda for each step.

From the 14 steps and selected measurements, 8 discriminant functions were created.

Table 5.141 shows the functions and calculated eigenvalues.

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation
1	73.043[a]	86.2	86.2	.993
2	8.109[a]	9.6	95.7	.944
3	1.945[a]	2.3	98.0	.813
4	1.307[a]	1.5	99.6	.753
5	.133[a]	.2	99.7	.343
6	.109[a]	.1	99.8	.313
7	.105[a]	.1	100.0	.308
8	.027[a]	.0	100.0	.161

Table 5.141. Eigenvalues of the discriminant functions created by analysis. The first 8 canonical discriminant functions were used in the analysis.

The 8 functions created by the analysis explain 100% of the variance, as do the first 7. Function 1 accounts for the most variation (86.2%). Function 2 explains less variation (9.6%), as does function 3 (2.3%) and 4 (1.5%). The remaining functions explain a very small proportion of the data.

The significance of the functions was tested by Wilks' Lambda and Chi-square tests, to indicate how well the functions separate the cases into the species groups. Table 5.142 shows the result.

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
1 through 8	.000	2709.924	112	.0001
2 through 8	.011	1381.942	91	.0001
3 through 8	.103	700.395	72	.0001
4 through 8	.304	367.221	55	.0001
5 through 8	.702	109.290	40	.0001
6 through 8	.795	70.700	27	.0001

7 through 8	.882	38.816	16	.001
8	.974	8.148	7	.320

Table 5.142. Wilks' Lambda and Chi-square analysis of discriminant functions for the Pleistocene and modern species DFA. Significance indicated by $p<0.05$.

Functions 1 through 8 have the greatest discriminatory ability (small Wilks' Lambda). The Chi-square test found all but function 8 as significant ($p<0.05$). All variability was explained by 1-8.

The structure matrix, indicating correlations between measurement and function are shown in Table 5.143.

	Function							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
UP3L	**.479***	.142	-.221	-.139	**-.415**	.126	-.177	**.374**
m1m2D	**.440***	-.186	.142	.210	**.406**	.219	.240	-.238
UP4W	**.431***	-.082	-.064	.150	**-.289**	.192	-.043	.141
p2p4L	**.426***	.209	-.095	**-.364**	.127	.134	.104	**-.281**
m1W	**.390***	.001	.074	.211	-.260	**-.362**	.217	**-.327**
p4L	**.384***	.019	-.035	**-.343**	-.098	-.132	**.339**	.170
p3p4B	**.350***	-.217	.193	.197	-.168	.179	**.261**	-.116
p3p4D[a]	.286*	-.008	.110	-.001	.086	.161	.197	-.163
m1m2B[a]	.284*	-.075	.034	.037	.143	.144	.175	-.065
UM1W[a]	.260*	.137	.233	.097	.018	.005	-.130	.048
m2W[a]	.200*	.041	.085	.171	.095	.043	-.091	.122
UM2W	**.310**	**.666***	-.123	**.506**	-.021	-.181	.028	**.344**
m2L	.241	**.372***	**.318**	.033	.194	.176	**-.348**	**-.269**
UM1M2L	**.338**	**.287**	**.645***	.098	**-.411**	.058	.033	-.022
UM1L	**.320**	-.016	**.522***	-.040	.094	-.316	-.142	**.418**
m1Ltal[a]	.068	.074	.146*	.050	-.082	-.060	-.069	-.053
m1Ltrig	**.471**	-.137	-.037	.086	-.188	**-.552***	**-.320**	-.272
p1p4L	**.440**	.154	.049	**-.413**	**.337**	-.093	**.452***	.043
p4W	**.353**	-.080	.007	.026	.027	.311	.082	**.376***

Table 5.143. Structure matrix showing the pooled within-groups correlations between the discriminating variables and standardised canonical discriminant functions. Correlations of <0.25 ignored due to low correlation. *Largest absolute correlation between each variable and any discriminant function, [a] indicates measurements that have not been selected in the analysis.

For function 1, P3L, m1Ltrig, m1m2D, p1p4L, P4W, p2p4L, m1W, p4L, p4W, p3p4B, M2W, M1M2L and M1L are the most highly correlated measurements. For function 2, M2W, m2L, M1M2L are highly correlated. For function 3, although of less importance, are M1M2L, M1L are highly correlated, for function 4, M2W, p1p4L, p2p4L, p4L. The remaining functions explain relative little variation in the dataset, and will not be focussed on further.

The group centroids for each group can also be used in describing separation (Table 5.144).

Species	Function							
	1	2	3	4	5	6	7	8
1	9.469	.417	-.132	.604	.038	.044	.065	.007
2	-.520	1.979	-1.356	-1.328	-.766	-.012	-.352	-.195
3	2.400	2.418	.703	-3.122	.051	-.309	.119	.490
4	-3.001	2.691	-1.269	-2.353	1.329	-.218	.162	-.444
5	-11.930	3.396	2.004	.142	-.196	.488	.556	-.063
6	-10.436	.806	-.956	.717	.338	.417	-.584	.159
7	-11.544	.618	-.742	1.440	-.078	-.763	.164	.033
8	-4.685	-7.294	-1.224	-.727	-.069	.198	.321	.016
9	-.572	-3.302	3.503	-.223	.046	-.234	-.452	-.106

Table 5.144. Functions at group centroids for the Pleistocene and modern species DFA. Unstandardised canonical discriminant functions evaluated at group means.

The group centroids describe each group in terms of the overall means of the measurements. Figure 5.82 illustrates the individual canonical scores and group centroids for discriminant functions 1 and 2.

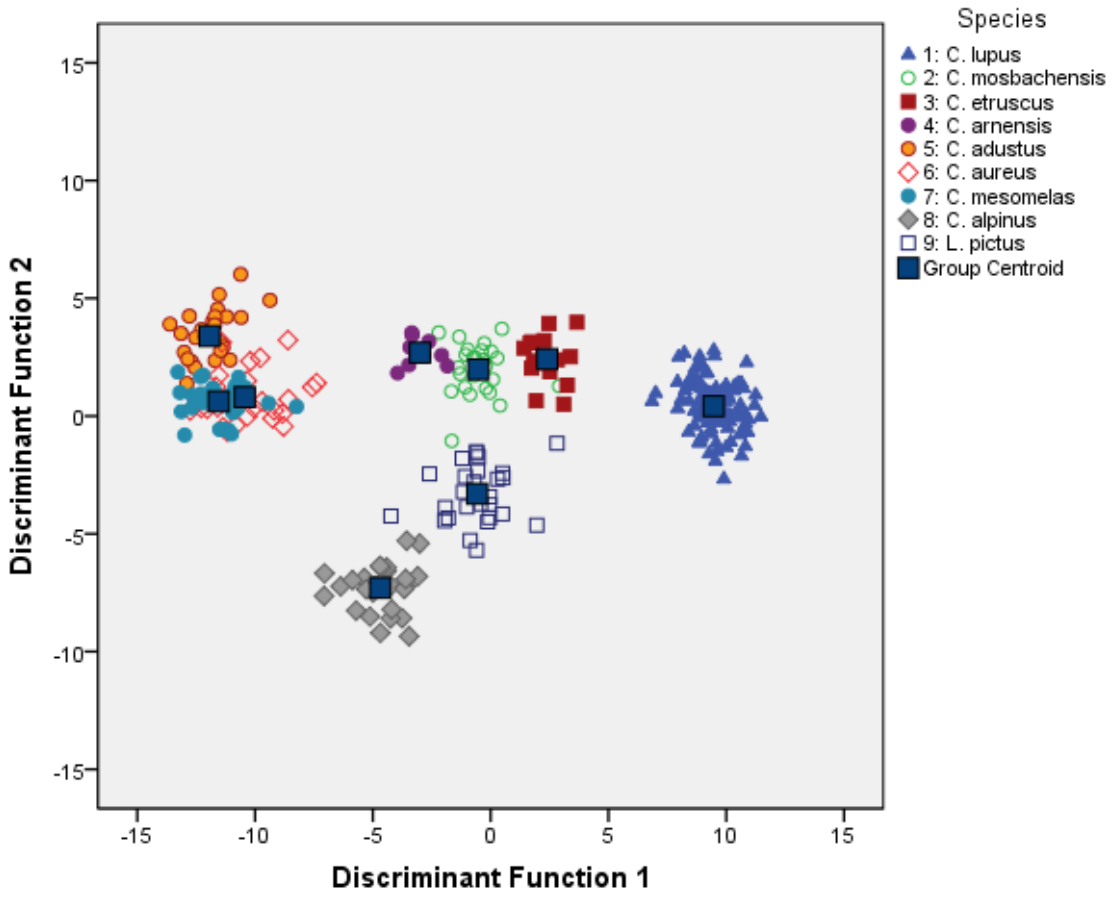


Figure 5.82. Plot of individual canonical scores and group centroids on the first and second discriminant functions from the discriminant analysis of dietary measurements for Pleistocene and modern species groups.

Function 1 explained 86.2% of the variation, with P3L, m1Ltrig, m1m2D, p1p4L, P4W, p2p4L, m1W, p4L, p4W, p3p4B, M2W, M1M2L and M1L as the most correlated

measurements. Function 1 clearly separated *C. lupus*, *C. etruscus, C. mosbachensis*, *C. alpinus* and *L. pictus*, and groups the jackals (*C. aureus, C. adustus* and *C. mesomelas*) together.

Function 1 indicates *C. lupus* as having the longest P3, the longest carnassial blades, with wide upper carnassials, plus deeper jaws at the molars combined with being broader at the premolars, longest premolar row, largest p4 and large upper molar complex than all the other analysed canids. In contrast, as the species separated the most from *C. lupus*, the jackal group has comparatively shorter and narrower versions of these measurements, plus shallower and narrower jaws.

The centrally positioned group containing *C. etruscus, C. mosbachensis, C. arnensis*, *L. pictus* and to some extent *C. alpinus*, are indicated as having smaller versions of these measurements than *C. lupus*, yet larger than in the jackal group. However, within this group *C. etruscus* was most separated from *C. alpinus* and *C. arnensis*, with both *C. mosbachensis* and *L. pictus* plotted between them. This indicates that *C. etruscus* has longer and wider versions of the measurements in comparison to the other Pleistocene canids, as well as *L. pictus* and *C. alpinus*.

Function 2 explains only 9.6% of the variation, with M2W, m2L and M1M2L as the most correlated measurements. Separation is clear between *C. alpinus* and *L. pictus* with the remaining canids. As the most separated species, *C. alpinus* is indicated as having the narrowest M2 and m2, with the most reduced buccal length of the upper molar complex in comparison to all other species. *L. pictus* similarly has reduced molars, albeit slightly less so than in *C. alpinus*.

For the remaining canids, *C. lupus* was slightly separated from the other Pleistocene canids as well as from *C. adustus*. Both *C. aureus* and *C. mesomelas* were separated similarly to *C. lupus*, indicating that the three species have similarly slightly reduced molars in comparison to *C. etruscus*, *C. mosbachensis C. arnensis* and *C. adustus*.

C. adustus was the most separated from *C. alpinus* and *L. pictus* on function 2, as well as also being separated from both *C. aureus* and *C. mesomelas*. *C. adustus* was therefore indicated as having the longest m2 and widest M2, with the longest buccal lengths of the molar complex in comparison. Both *C. arnensis* and *C. etruscus* are separated along with *C. adustus* by function 2. Using the 3 discriminant functions, the variation in the discriminant analysis model can be summarised by Table 5.145.

			Predicted Group Membership									
		Species	1	2	3	4	5	6	7	8	9	Total
Original	Count	1	121	0	0	0	0	0	0	0	0	121
		2	0	27	1	1	0	0	0	0	0	29
		3	0	1	15	0	0	0	0	0	0	16
		4	0	0	0	11	0	0	0	0	0	11
		5	0	0	0	0	26	0	0	0	0	26
		6	0	0	0	0	0	26	5	0	0	31
		7	0	0	0	0	0	2	28	0	0	30
		8	0	0	0	0	0	0	0	30	0	30
		9	0	0	0	0	0	0	0	0	27	27
	%	1	100.0	.0	.0	.0	.0	.0	.0	.0	.0	100.0
		2	.0	93.1	3.4	3.4	.0	.0	.0	.0	.0	100.0
		3	.0	6.3	93.8	.0	.0	.0	.0	.0	.0	100.0
		4	.0	.0	.0	100.0	.0	.0	.0	.0	.0	100.0
		5	.0	.0	.0	.0	100.0	.0	.0	.0	.0	100.0
		6	.0	.0	.0	.0	.0	83.9	16.1	.0	.0	100.0
		7	.0	.0	.0	.0	.0	6.7	93.3	.0	.0	100.0
		8	.0	.0	.0	.0	.0	.0	.0	100.0	.0	100.0
		9	.0	.0	.0	.0	.0	.0	.0	.0	100.0	100.0
Cross-validated[a]	Count	1	121	0	0	0	0	0	0	0	0	121
		2	0	26	1	2	0	0	0	0	0	29
		3	0	2	14	0	0	0	0	0	0	16
		4	0	0	0	11	0	0	0	0	0	11
		5	0	0	0	0	26	0	0	0	0	26
		6	0	0	0	0	0	25	6	0	0	31
		7	0	0	0	0	0	2	28	0	0	30
		8	0	0	0	0	0	0	0	30	0	30

		9	0	0	0	0	0	0	0	0	27	27
	%	**1**	100.0	.0	.0	.0	.0	.0	.0	.0	.0	100.0
		2	.0	89.7	3.4	6.9	.0	.0	.0	.0	.0	100.0
		3	.0	12.5	87.5	.0	.0	.0	.0	.0	.0	100.0
		4	.0	.0	.0	100.0	.0	.0	.0	.0	.0	100.0
		5	.0	.0	.0	.0	100.0	.0	.0	.0	.0	100.0
		6	.0	.0	.0	.0	.0	80.6	19.4	.0	.0	100.0
		7	.0	.0	.0	.0	.0	6.7	93.3	.0	.0	100.0
		8	.0	.0	.0	.0	.0	.0	.0	100.0	.0	100.0
		9	.0	.0	.0	.0	.0	.0	.0	.0	100.0	100.0

Table 5.145. Classification of results based on stepwise selected measurements and created discriminant functions. a. Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*, 5: *C. adustus*, 6: *C. aureus*, 7: *C. mesomelas*, 8: *C. alpinus*, 9: *L. pictus*.

Based on the original selected data, 100% of cases were classified correctly as *C. lupus, C. arnensis*, *C. adustus*, *C. alpinus* and *L. pictus*. For *C. mosbachensis*, 93.1% were correctly classified, with cases wrongly classified as *C. arnensis* and *C. etruscus*. For *C. etruscus*, 93.8% were correctly classified, with cases wrongly classified as *C. mosbachensis* only. For *C. aureus*, 83.9% were correctly classified with wrongly classified cases as *C. mesomelas*. For *C. mesomelas*, 93.3% were correctly classified, with wrongly classified cases as *C. aureus*.

The stepwise discriminant model therefore correctly classified 96.9% of cases to their species groups, however, as this is based on the cases themselves to create the model, it may be an over-optimistic result. To correct this, cross-validation was used, and again 100% of cases were correctly classified as *C. lupus, C. arnensis, C. adustus, C. alpinus* and *L. pictus.*

For *C. mosbachensis*, 89.7% were correctly classified, with wrongly classified cases in both *C. etruscus* and *C. arnensis*. For *C. etruscus*, 87.5% were correctly classified with wrongly classified cases in *C. mosbachensis*. For *C. aureus,* 80.6% were correctly classified, with wrongly classified cases in *C. mesomelas*. For *C. mesomelas*, 93.3% were correctly classified, with wrongly classified cases in *C. aureus*. Thus the cross-validated model correctly classified 96% of cases.

Summary

To summarise, the Pleistocene and modern species stepwise DFA correctly classified 96% of cases (based on cross-validation) for *C. adustus, C. aureus, C. mesomelas, C. alpinus, L. pictus, C. lupus, C. mosbachensis, C. arnensis* and *C. etruscus*. Function 1 explained the highest amount of variation (86.2%), and discriminated the species based on P3L, m1Ltrig, m1m2D, p1p4L, P4W, p2p4L, m1W, p4L, p4W, p3p4B, M2W, M1M2L and M1L. Function 2, although explaining a lower proportion of the variation (9.6%), discriminated the species by M2W, m2L and M1M2L.

5.3.7. Morphometric ratios

Although linear measurements have been preferentially analysed throughout, dietary specific morphometric ratios were calculated for comparison. Ratios were chosen to reflect bone consumption, flesh slicing and both lower and upper crushing mechanisms. The ratios were then examined for the presence of temporal and species differences.

5.3.7.1. Temporal analysis of dietary ratios

The morphometric ratios of PMD, RBL, RLGA, UM2/1 were calculated for MIS 3, 5a and 7 in Britain.

5.3.7.1.1. PMD

PMD represents the ratio of p4 width over length, indicating p4 shape. Figure 6.83 illustrates PMD between MIS 3, 5a and 7.

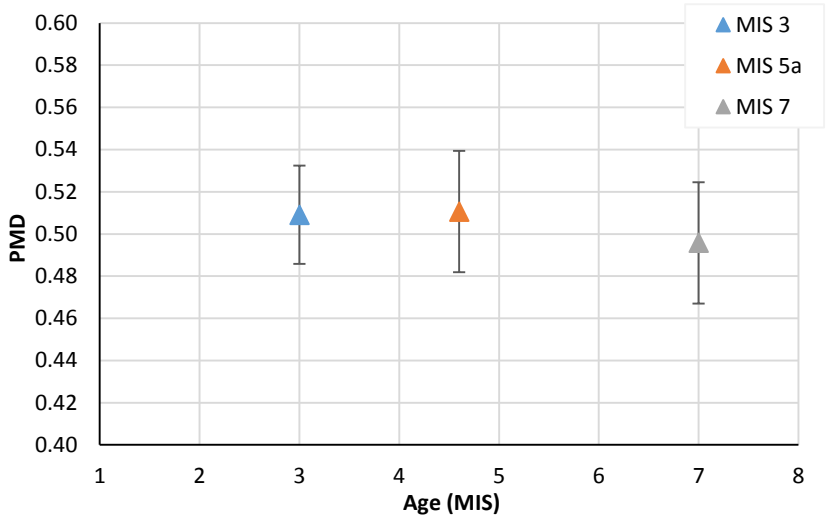


Figure 5.83. PMD mean and standard deviation for *C. lupus* from MIS 3, 5a and 7 in Britain.

PMD in *C. lupus* from MIS 3, 5a and 7 shows little temporal variation. MIS 3 and 5a have similar mean values, with MIS 7 slightly lower, yet within the variation for the younger age groups. It is of note that temporal differences were found in the raw measurements of p4 length and width, yet when combined as a ratio for p4 shape, variation is lost.

PMD was analysed for temporal differences using one-way ANOVA. Table 5.146 shows the results.

Ratio	MIS	n	Mean	SD	Levene's test	one-way ANOVA
PMD	3	17	0.509	0.023	$F_{(2, 50)} = 0.721$, $p=0.491$	$F_{(2, 50)} = 0.837$, $p=0.439$
	5a	29	0.511	0.029		
	7	7	0.496	0.031		

Table 5.146. Results from Levene's test and one-Way ANOVA of PMD between MIS 3, 5a and 7. Significance indicated by $p<0.05$.

- Levene's test was non-significant, indicating equal variances.

- One-way ANOVA was non-significant, indicating no differences in PMD across the age groups. Hence, PMD does not vary temporally, in contrast to the same analysis of the raw measurements of p4.

5.3.7.1.2. RBL

RBL is the ratio of m1 trigonid length over whole m1 length, indicating flesh slicing ability by quantifying the proportion of m1 utilised as a cutting blade. Figure 5.84 illustrates RBL for *C. lupus* from MIS 3, 5a and 7.

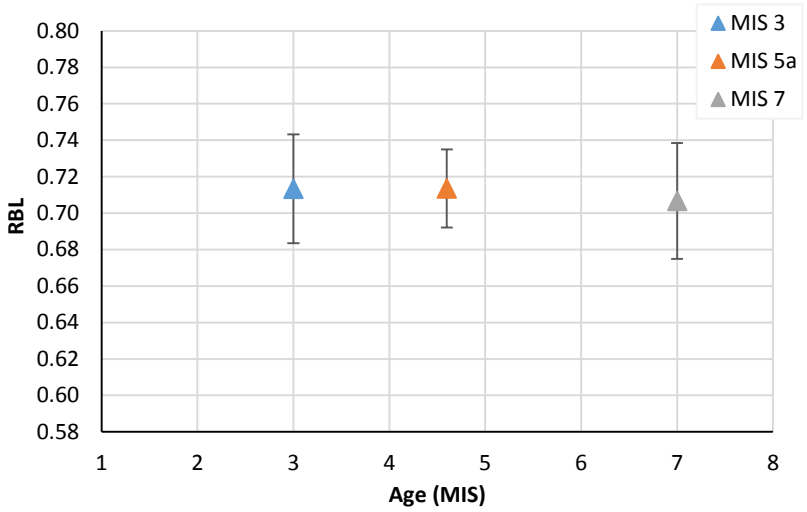


Figure 5.84. RBL mean and standard deviation for *C. lupus* from MIS 3, 5a and 7 in Britain.

The mean RBL values are similar, and do not vary temporally. All age groups have similar variation in RBL. Again temporal differences were found in the raw measurement of m1Ltrig, yet when combined as a ratio, variation was lost.

RBL was analysed for temporal differences using one-way ANOVA. Table 5.147 shows the results.

Ratio	MIS	n	Mean	SD	Levene's test	one-way ANOVA
RBL	3	20	0.713	0.030	$F_{(2, 44)} = 0.433$, $p=0.651$	$F_{(2, 44)} = 0.232$, $p=0.794$
	5a	18	0.714	0.021		
	7	9	0.707	0.032		

Table 5.147. Results from Levene's test and one-Way ANOVA of RBL between MIS 3, 5a and 7. Significance indicated by $p<0.05$.

- Levene's test was non-significant, indicating equal variances.
- One-way ANOVA was non-significant, indicating no differences in RBL across the age groups. Thus, RBL also does not vary temporally, in contrast to the same analysis of the raw measurement of m1Ltrig.

5.3.7.1.3. RLGA

RLGA is the ratio of the square root of the summed areas of m1 talonid and m2, over m1 trigonid length, indicating the relationship between the size of the mandible crushing apparatus, with the main flesh slicing tool (m1 trigonid). Figure 5.85 illustrates the RLGA for *C. lupus* from MIS 3, 5a and 7.

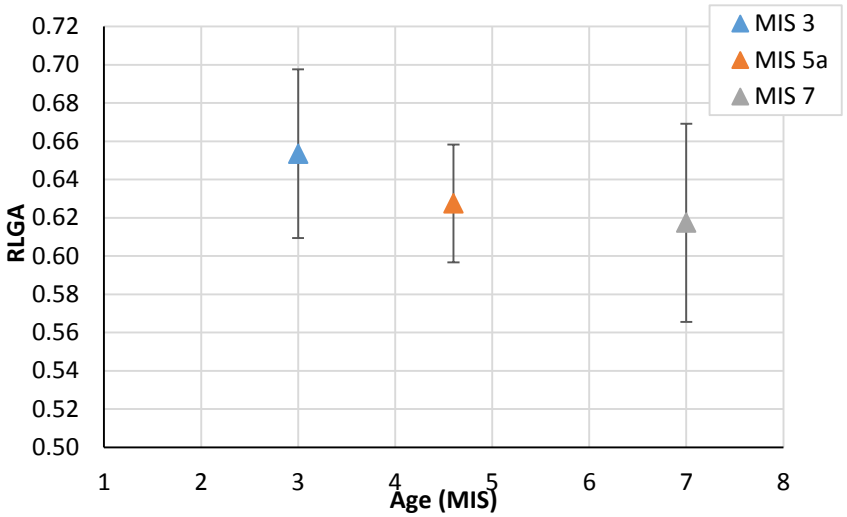


Figure 5.85. RLGA mean and standard deviation for *C. lupus* from MIS 3, 5a and 7 in Britain.

RLGA between MIS 3, 5a and 7 is slightly temporally varied. The mean of MIS 3 is highest, followed by lower values for both MIS 5a and 7, however, they are within range of the variation for each age group. In contrast, m1Ltal, m2L, m2W were non-significant in the temporal analysis of the raw measurements, whereby only m1Ltrig was significant.

RLGA was analysed for temporal differences using one-way ANOVA. Table 5.148 shows the results.

Ratio	MIS	n	Mean	SD	Levene's test	one-way ANOVA
RLGA	3	10	0.654	0.044	$F_{(2, 23)} = 1.633$, $p=0.217$	$F_{(2, 23)} = 1.708$, $p=0.203$
	5a	11	0.627	0.031		
	7	5	0.617	0.052		

Table 5.148. Results from Levene's test and one-Way ANOVA of RLGA between MIS 3, 5a and 7. Significance indicated by $p<0.05$.

- Levene's test was non-significant, indicating equal variances.
- One-way ANOVA found RLGA as non-significant, indicating no temporal differences in RLGA.

5.3.7.1.4. UM2/1

UM2/1 is the ratio if the square root of M2 area, over the square root of M1 area, indicating the relationship between the size of the upper molar areas. Figure 5.86 illustrates UM2/1 for *C. lupus* from MIS 3, 5a and 7.

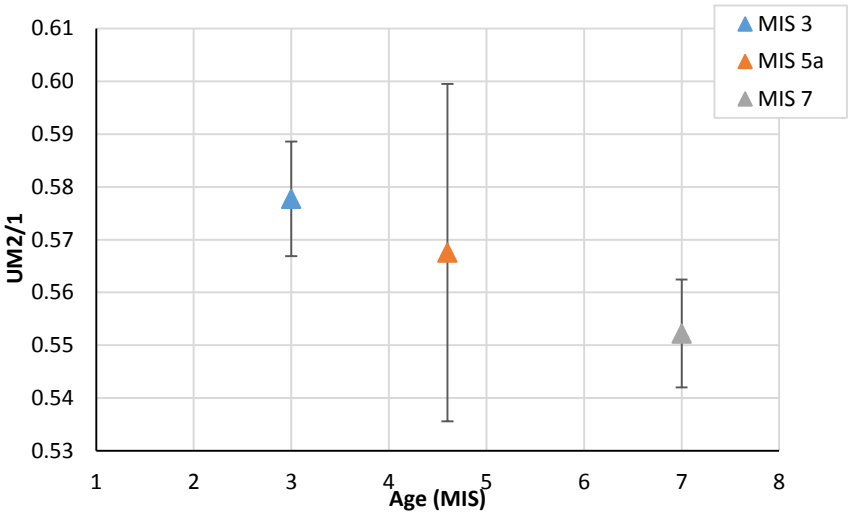


Figure 5.86. UM2/1 mean and standard deviation for *C. lupus* from MIS 3, 5a and 7 in Britain.

UM2/1 between MIS 3, 5a and 7 varies temporally, with UM2/1 in wolves from MIS 3 having larger values than in MIS 7. MIS 5a has the highest level of variation, which is within range for both age groups. The raw measurements of M1L and M1W, and M2W were found to be non-significant.

UM2/1 was analysed for temporal differences using one-way ANOVA. Table 5.149 shows the results.

Ratio	MIS	n	Mean	SD	Levene's test	one-way ANOVA
UM2/1	3	3	0.578	0.011	$F_{(2, 10)} = 2.324$, p=0.148	$F_{(2, 10)} = 0.749$, p=0.498
	5a	7	0.568	0.032		
	7	3	0.552	0.025		

Table 5.149. Results from Levene's test and one-Way ANOVA of UM2/1 between MIS 3, 5a and 7. Significance indicated by p<0.05.

- Levene's test was non-significant indicating equal variances.
- One-way ANOVA was non-significant, indicating no temporal differences in UM2/1 across the age groups.

Summary

In contrast to the temporal analysis of linear measurements, no temporal variation was present in the morphometric ratios of PMD, RBL, RLGA and UM2/1 between MIS 3, 5a and 7 *C. lupus* from Britain.

5.3.7.2. Species analysis

The presence of differences between the canid species in the same morphometric ratios was explored. Once again this analysis will focus on smaller groupings of the Pleistocene species, namely *C. lupus* from MIS 3, 5a and 7 in Britain, *C. mosbachensis* from the late Early Pleistocene of Untermassfeld, and *C. arnensis* and *C. etruscus* from the Upper Valdarno Basin.

5.3.7.2.1. PMD

Figure 5.87 illustrates the mean and standard deviation for PMD in the four analysed species.

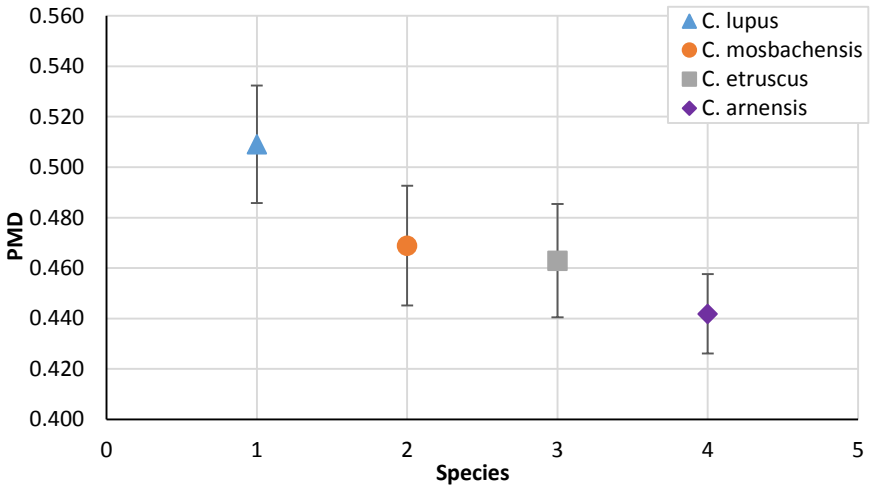


Figure 5.87. PMD mean and standard deviation for Pleistocene *C. lupus* (1), *C. mosbachensis* (2), *C. etruscus* (3) and *C. arnensis* (4).

C. lupus has the largest PMD, although with slight overlap in the lower values of its variation. *C. etruscus* and *C. mosbachensis* are very similar, with *C. arnensis* having the smaller mean PMD value.

PMD was analysed using one-way ANOVA for the four species groups. Table 5.150 shows the results.

Ratio	Species	n	Mean	SD	Levene's test	one-way ANOVA
PMD	1	53	0.508	0.027	$F_{(3, 82)} = 0.768$, p=0.515	$F_{(3, 82)} = 30.828$, p=0.0001
	2	12	0.461	0.024		
	3	11	0.494	0.0225		
	4	10	0.442	0.016		

Table 5.150. Results from Levene's test and one-way ANOVA for PMD and species groups. Number (n), mean and SD (standard deviation) shown. Species groups: 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Levene's test was non-significant, indicating equal variances.
- One-way ANOVA found PMD as significant, indicating differences between the species.

Post hoc tests using Tukey HSD were carried out for multiple comparisons. Table 5.151 shows the results.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	.047570*	.008062	.0001	.02643	.06871
	3	.045244*	.008355	.0001	.02333	.06716
	4	.066353*	.008694	.0001	.04355	.08915
2	1	-.047570*	.008062	.0001	-.06871	-.02643
	3	-.002326	.010527	.996	-.02993	.02528
	4	.018783	.010798	.310	-.00953	.04710
3	1	-.045244*	.008355	.0001	-.06716	-.02333
	2	.002326	.010527	.996	-.02528	.02993
	4	.021109	.011019	.229	-.00779	.05001
4	1	-.066353*	.008694	.0001	-.08915	-.04355
	2	-.018783	.010798	.310	-.04710	.00953
	3	-.021109	.011019	.229	-.05001	.00779

Table 5.151. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for PMD in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Tukey HSD found PMD for *C. lupus* as significantly different from all other species.
- Comparisons of *C. mosbachensis*, *C. etruscus* and *C. arnensis* were all non-significant.

5.3.7.2.2: RBL

Figure 5.88 illustrates RBL for the four canid species.

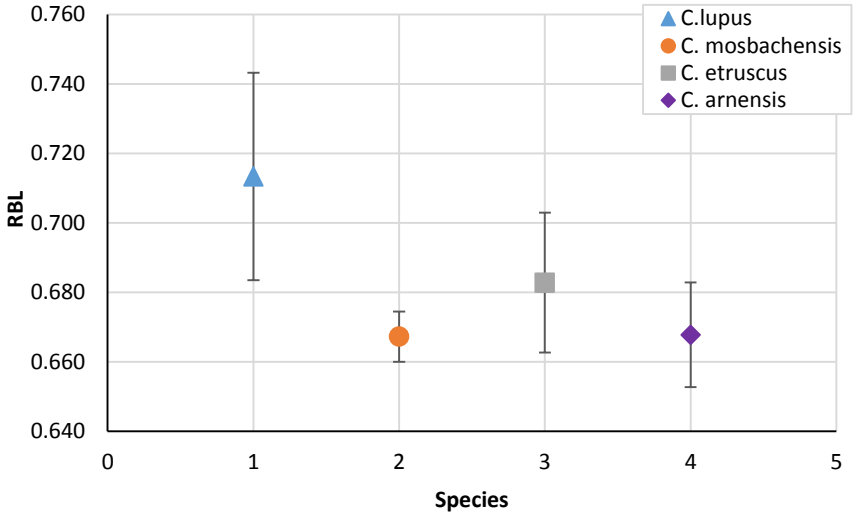


Figure 5.88. RBL mean and standard deviation for Pleistocene *C. lupus* (1), *C. mosbachensis* (2), *C. etruscus* (3) and *C. arnensis* (4).

C. lupus has the largest mean RBL and highest variation, overlapping with *C. etruscus*. *C. etruscus* has larger RBL values than both *C. mosbachensis* and *C. arnensis*, which are similarly low, albeit both within range of *C. etruscus*.

RBL was analysed using one-way ANOVA for the four species groups. Table 5.152 shows the results.

Ratio	Species	n	Mean	SD	Levene's test	one-way ANOVA
RBL	1	47	0.712	0.027	$F_{(3, 73)} = 3.787$, p=0.014	$F_{(3, 73)} = 18.607$, p=0.0001
	2	10	0.667	0.007		
	3	10	0.683	0.020		
	4	10	0.668	0.015		

Table 5.152. Results from Levene's test and one-way ANOVA for RBL and species groups. Number (n), mean and SD (standard deviation) shown. Species groups: 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Levene's test was significant, indicating unequal variances between the species groups. As the linear measurement data are normally distributed, violation of equal variance is not an issue, and the one-way result will be used.
- One-way ANOVA found PMD as significant, indicating differences between the species.

Post hoc tests using Dunnett's T3 (for unequal variances) were carried out enabling multiple comparisons. Table 5.153 shows the results.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	.044729*	.004510	.0001	.03242	.05704
	3	.029129*	.007467	.007	.00706	.05120

	4	.044329*	.006159	.0001	.02672	.06193
2	1	-.044729*	.004510	.0001	-.05704	-.03242
	3	-.015600	.006743	.197	-.03671	.00551
	4	-.000400	.005258	1.000	-.01650	.01570
3	1	-.029129*	.007467	.007	-.05120	-.00706
	2	.015600	.006743	.197	-.00551	.03671
	4	.015200	.007941	.339	-.00826	.03866
4	1	-.044329*	.006159	.0001	-.06193	-.02672
	2	.000400	.005258	1.000	-.01570	.01650
	3	-.015200	.007941	.339	-.03866	.00826

Table 5.153. Results of *post hoc* one way ANOVA using Dunnett's T3 correction for multiple comparisons for RBL in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*.

- Dunnett's T3 found RBL for *C. lupus* as significantly different from all other species groups.
- Comparisons of *C. mosbachensis*, *C. etruscus* and *C. arnensis* were non-significant.

5.3.7.2.3. RLGA

Figure 5.89 illustrates RLGA for the four canid species.

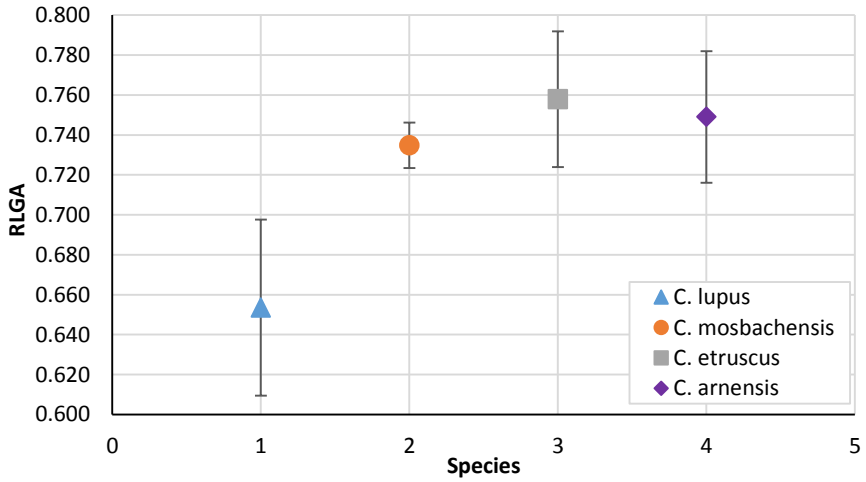


Figure 5.89. RLGA mean and standard deviation for Pleistocene *C. lupus* (1), *C. mosbachensis* (2), *C. etruscus* (3) and *C. arnensis* (4).

In contrast to PMD and RBL, RLGA for *C. lupus* is smaller than in the other species. *C. etruscus* has the largest RLGA value, although its variation also encompasses *C. mosbachensis* and *C. arnensis*.

RLGA was analysed using one-way ANOVA for the four species groups. Table 5.154 shows the results.

Ratio	Species	n	Mean	SD	Levene's test	one-way ANOVA
RLGA	1	26	0.636	0.042	$F_{(3, 48)} = 3.409$, p=0.025	$F_{(3, 48)} = 42.302$, p=0.0001
	2	8	0.735	0.011		
	3	8	0.758	0.034		
	4	10	0.749	0.033		

Table 5.154. Results from Levene's test and one-way ANOVA for RLGA and species groups. Number (n), mean and SD (standard deviation) shown. Species groups: 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by p<0.05.

- Levene's test was significant, indicating unequal variances between the species groups. As previous, since linear measurements used in RLGA were normally distributed, one-way result will be kept.
- One-way ANOVA found RLGA as significant, indicating differences between the species.

Subsequent *Post hoc* tests using Dunnett's T3 (as unequal variances). Table 5.155 shows the results.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	-.099173*	.009133	.0001	-.12469	-.07366
	3	-.122298*	.014526	.0001	-.16613	-.07847
	4	-.113323*	.013225	.0001	-.15151	-.07514
2	1	.099173*	.009133	.0001	.07366	.12469
	3	-.023125	.012672	.418	-.06504	.01879
	4	-.014150	.011157	.744	-.04887	.02057
3	1	.122298*	.014526	.0001	.07847	.16613
	2	.023125	.012672	.418	-.01879	.06504
	4	.008975	.015877	.992	-.03860	.05655
4	1	.113323*	.013225	.0001	.07514	.15151
	2	.014150	.011157	.744	-.02057	.04887
	3	-.008975	.015877	.992	-.05655	.03860

Table 5.155. Results of *post hoc* one way ANOVA using Dunnett's T3 for multiple comparisons for RLGA in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by p<0.05.

- Dunnett's T3 found RLGA in *C. lupus* as significantly different from all other species.
- Comparisons of *C. mosbachensis*, *C. etruscus* and *C. arnensis* were non-significant.

5.3.7.2.4. UM2/1

Figure 5.90 illustrates UM2/1 for the four canid species.

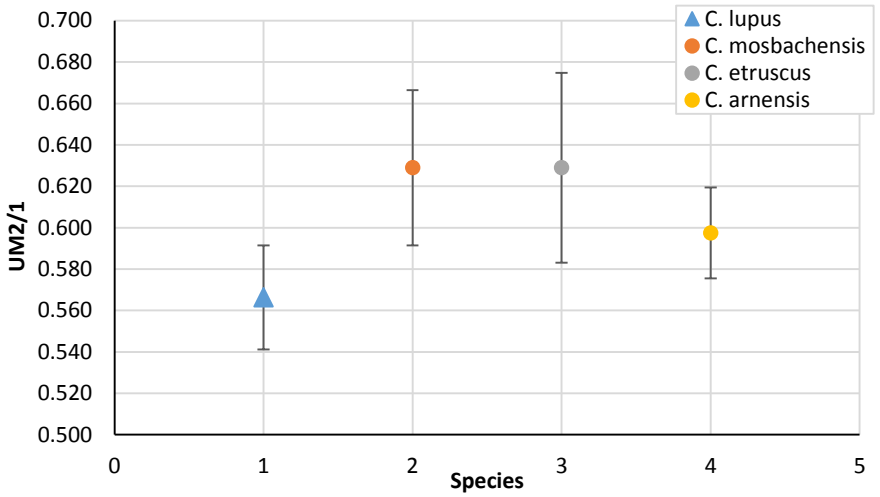


Figure 5.90. UM2/1 mean and standard deviation for Pleistocene *C. lupus* (1), *C. mosbachensis* (2), *C. etruscus* (3) and *C. arnensis* (4).

Like RLGA, UM2/1 is smaller in *C. lupus* than in the other species. Both *C. mosbachensis* and *C. etruscus* have similar mean values and variation. *C. arnensis* has slightly smaller mean UM2/1 than both *C. mosbachensis* and *C. etruscus*, although still within their variation range.

UM2/1 was analysed using one-way ANOVA for the four species groups. As *C. etruscus* from Upper Valdarno basin contained only 1 individual, those from Olivola were also included. Table 5.156 shows the results.

Ratio	Species	n	Mean	SD	Levene's test	one-way ANOVA
UM2/1	1	13	0.566	0.025	$F_{(3, 20)} = 0.571$, p=0.641	$F_{(3, 20)} = 4.621$, p=0.013
	2	3	0.629	0.038		
	3	4	0.558	0.046		
	4	4	0.598	0.022		

Table 5.156. Results from Levene's test and one-way ANOVA for UM2/1 and species groups. Number (n), mean and SD (standard deviation) shown. Species groups: 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*. Significance indicated by $p<0.05$.

- Levene's test was non-significant, indicating equal variances.
- One-way ANOVA found UM2/1 significant, indicating differences between the species.

Post hoc tests using Tukey HSD were carried out, Table 5.157 shows the results.

Species	Species	Mean Difference	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	-.062282*	.019291	.020	-.11628	-.00829
	3	.008385	.017221	.961	-.03982	.05659
	4	-.031115	.017221	.299	-.07932	.01709
2	1	.062282*	.019291	.020	.00829	.11628

	3	.070667*	.023004	.028	.00628	.13505
	4	.031167	.023004	.541	-.03322	.09555
3	1	-.008385	.017221	.961	-.05659	.03982
	2	-.070667*	.023004	.028	-.13505	-.00628
	4	-.039500	.021297	.278	-.09911	.02011
4	1	.031115	.017221	.299	-.01709	.07932
	2	-.031167	.023004	.541	-.09555	.03322
	3	.039500	.021297	.278	-.02011	.09911

Table 5.157. Results of *post hoc* one way ANOVA using Tukey HSD for multiple comparisons for UM2/1 in the species groups. *Mean difference is significant at 0.05 level. Species 1: *C. lupus*, 2: *C. mosbachensis*, 3: *C. etruscus*, 4: *C. arnensis*.

- Tukey HSD found UM2/1 for *C. lupus* as significantly different from *C. mosbachensis*, yet non-significant with both *C. etruscus* and *C. arnensis*.
- *C. mosbachensis* was significantly different from *C. etruscus*, and similar to *C. arnensis*.
- *C. etruscus* was also similar to *C. arnensis*.

Summary

Between the Pleistocene species, PMD, RBL and RLGA only found differences in *C. lupus*. In contrast, UM2/1 was the only ratio to differentiate between the earlier Pleistocene canids, perhaps reflecting the importance in upper molar shape in *C. mosbachensis, C. etruscus* and *C. arnensis*.

5.3.8. Tooth breakage

Analysis of tooth breakage was carried out on *C. lupus* from Pleistocene Britain and Europe, as well as for *C. mosbachensis, C. etruscus* and *C. arnensis*.

5.3.8.1. Tooth breakage analysis: *C. lupus* from Britain

All broken teeth were counted and tabulated (Table 5.158) for *C. lupus* from Britain.

Site	Site code	MIS	Tot. n teeth	Tot. n broken teeth	% broken teeth	Tot. n unbroken teeth
Cae Gywn Cave	**CGC**	2	5	0	0	5
Ogof yr Ychen	**OGF**	2	7	0	0	7
Tot. MIS 2		*2*	*12*	*0*	*0*	*12*
Black Rock Quarry	**BRQ**	3	23	0	0	23
Kent's Cavern (Cave Earth)	**KC**	3	24	1	4.2	23
Oreston Cave	**OSTN**	3	44	2	4.6	42

Paviland	**PAV**	3	32	1	3.1	31
Pin Hole Cave	**PHC**	3	32	0	0	32
Sandford Hill	**SFH**	3	4	0	0	4
Uphill Cave	**UPH**	3	2	0	0	2
Tot. MIS 3		*3*	*161*	*4*	*2.5*	*157*
Banwell Bone Cave	**BWL**	5a	125	12	9.6	113
Bosco's Den	**BSD**	5a	23	2	8.7	21
Steetley Quarry	**STQ**	5a	4	0	0	4
Stump Cross Cave	**SCC**	5a	8	0	0	8
Windy Knoll	**WK**	5a	19	1	5.3	18
Wretton	**WTN**	5a	8	0	0	8
Tot. MIS 5a		*5a*	*187*	*15*	*8.0*	*172*
Bacon Hole	**BH**	5c	5	1	20.0	4
Minchin Hole	**MCN**	5c	2	1	50.0	1
Picken's Hole (Layer 5)	**PKN**	5c	2	0	0	2
Tot. MIS 5c		*5c*	*9*	*2*	*22.2*	*7*
Barrington	**BTN**	5e	2	1	50.0	1
Joint Mitnor Cave	**JMC**	5e	47	1	2.1	46
Tot. MIS 5e		*5e*	*49*	*2*	*4.1*	*47*
Clevedon Cave	**CVD**	6	39	3	7.7	36
Tot. MIS 6		*6*	*39*	*3*	*7.7*	*36*
Crayford	**CYD**	7	7	1	14.3	6
Hutton Cave	**HTN**	7	28	1	3.6	27
Ilford	**ILF**	7	5	0	0	5
Marsworth	**MRSW**	7	9	0	0	9
Pontnewydd Cave (L. Breccia & Int. Layer)	**PNC**	7	24	0	0	24
Tornewton Cave Otter Stratum	**TNC OS**	7	3	0	0	3
Tot. MIS 7		*7*	*76*	*2*	*2.6*	*74*

Table 5.158. Counts of broken teeth of *C. lupus* from Britain. Total number of teeth, number of broken teeth, percentage broken teeth and number of unbroken teeth shown. Totals for age groups shown in italics.

MIS 5a contains the highest number of broken teeth (Table 5.158), whilst MIS 2 is the only age group containing no broken teeth, although this may relate to low numbers of teeth represented. Age groups containing the highest numbers of broken teeth will be analysed further. Figure 5.91 illustrates the percentage of broken teeth present in sites of MIS 3 age for *C. lupus*.

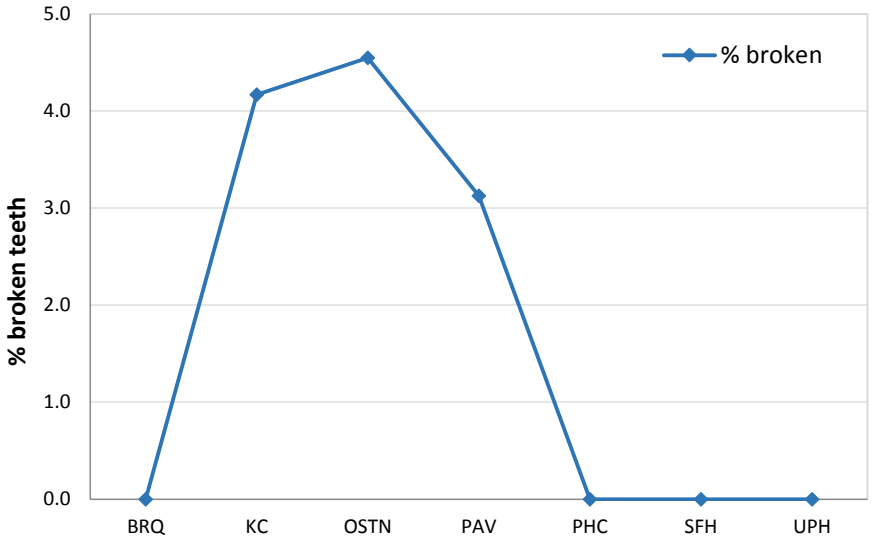


Figure 5.91. Percentage of broken teeth present in sites of MIS 3 for *C. lupus*. See Table 5.158 for site codes.

Out of the 7 sites of MIS 3, only 3 sites contained broken teeth, with Oreston Cave having the highest percentage. Figure 5.92 illustrates the percentage of broken teeth present in sites of MIS 5a age for *C. lupus*.

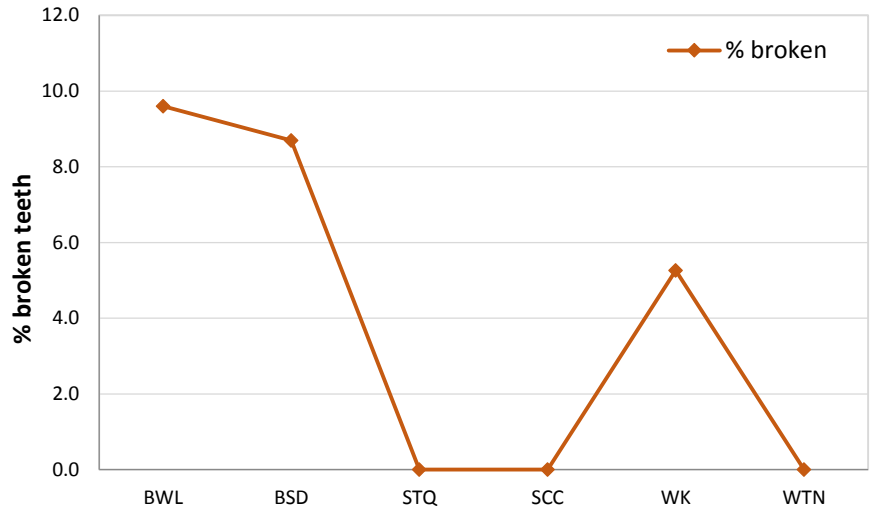


Figure 5.92. Percentage of broken teeth present in sites of MIS 5a for *C. lupus*. See Table 5.158 for site codes.

From the 6 sites of MIS 5a, only half contained broken teeth, of which Banwell Bone Cave contained the highest percentage. Figure 5.93 illustrates the percentage of broken teeth present in sites of MIS 7 for *C. lupus.*

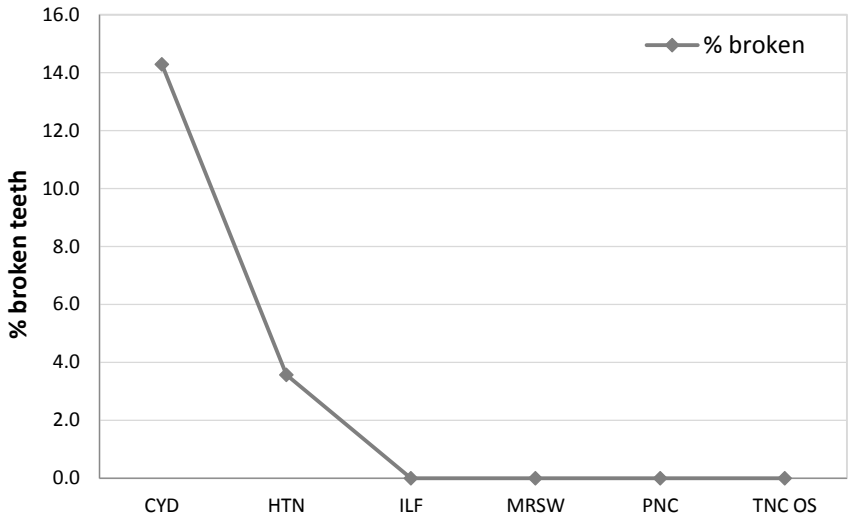


Figure 5.93. Percentage of broken teeth present in sites of MIS 7 age for *C. lupus*. See Table 5.158 for site codes.

From the 6 sites of MIS 7, only 2 sites contained broken teeth, with Crayford containing the highest percentage. Figure 5.94 illustrates the overall percentage of broken teeth for *C. lupus* from MIS 3, 5a and 7.

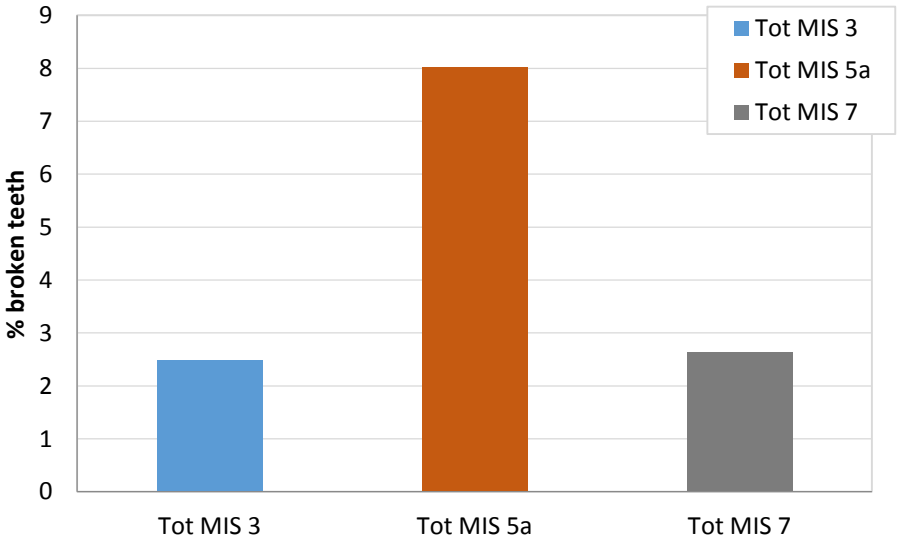


Figure 5.94. Percentage of broken teeth compared in *C. lupus* from MIS 3, 5a and 7 in Britain.

Overall, MIS 5a contains the highest percentage of broken teeth, with MIS 3 and 7 more similar.

5.3.8.1.1. Statistical analysis of tooth breakage

The frequency of tooth breakage within these age groups was examined for temporal variation. Pearson Chi-square tests were used to analyse the frequency of tooth breakage in MIS 3, 5a and 7, as these age groups had sufficiently high numbers of broken teeth.

MIS 3 and MIS 5a

To determine whether differences in the frequency of tooth breakage in age groups MIS 3 and 5a are significant, 2-way classification Chi square tests (using 2x2 contingency tables) were used. Table 5.159a, b shows the results.

			Broken		
			Broken 1	Unbroken 2	Total
Age group	MIS 3	Count	4	157	161
		Expected Count	8.8	152.2	161.0
	MIS 5a	Count	15	172	187
		Expected Count	10.2	176.8	187.0
Total		Count	19	329	348
		Expected Count	19.0	329.0	348.0

Table 5.159a. Cross-tabulation of age groups (MIS 3 and MIS 5a) and tooth breakage for *C. lupus* in Britain. Count and expected count shown. Numbers illustrated used in Chi-square analysis in Table 5.559b.

	Value	df	Asymp. Sig. (2-sided)	Exact Sig. (2-sided)	Exact Sig. (1-sided)
Pearson Chi-Square	5.138[a]	1	.023		
Continuity Correction[b]	4.122	1	.042		
Likelihood Ratio	5.523	1	.019		
Fisher's Exact Test				.031	.019
Linear-by-Linear Association	5.124	1	.024		
N of Valid Cases	348				

Table 5.159b. Results from the Chi-square test for tooth breakage and age groups (MIS 3 and MIS 5a) for *C. lupus* from Britain. a. 0 cells (.0%) have expected count less than 5. The minimum expected count is 8.79. Significance indicated by $p<0.05$.

The Pearson Chi-square for tooth breakage in MIS 3 and MIS 5a was significant ($\chi^2= 5.138$, $N = 348$, $p = 0.023$). As significant differences exist in the frequency distribution of tooth breakage, an association is present between breakage frequency and the age groups (MIS 3 and MIS 5a) in *C. lupus*, thus indicating that the tooth breakage is unusual, and may relate to temporal differences in diet.

MIS 3 and MIS 7

Table 5.160 a, b shows the results from 2-way classification Chi square tests (2x2 contingency tables) for tooth breakage in age groups MIS 3 and 7.

			Broken		
			Broken 1	Unbroken 2	Total
Age group	MIS 3	Count	4	157	161
		Expected Count	4.1	156.9	161.0
	MIS 7	Count	2	74	76
		Expected Count	1.9	74.1	76.0
Total		Count	6	231	237
		Expected Count	6.0	231.0	237.0

Table 5.160a. Cross-tabulation of age groups (MIS 3 and MIS 7) and tooth breakage for *C. lupus* in Britain. Count and expected count shown. Numbers illustrated used in Chi-square analysis in Table 5.160b.

	Value	df	Asymp. Sig. (2-sided)	Exact Sig. (2-sided)	Exact Sig. (1-sided)
Pearson Chi-Square	.005[a]	1	.946		
Continuity Correction[b]	.000	1	1.000		
Likelihood Ratio	.004	1	.947		
Fisher's Exact Test				1.000	.626
Linear-by-Linear Association	.005	1	.946		
N of Valid Cases	237				

Table 5.160b. Results from Chi-square test for tooth breakage and age groups (MIS 3 and MIS 7) for Britain *C. lupus*. a. 2 cells (50.0%) have expected count less than 5. The minimum expected count is 1.92. Significance indicated by $p<0.05$.

As more than 50% of cells have an expected count of <5, the result from the Fisher's Exact test was used. The Fisher's Exact test was non-significant (FET $p=1.000$), indicating no significant differences in the distribution of tooth breakage. Hence, no association was found between tooth breakage frequency in MIS 3 and MIS 7, and tooth breakage frequency is not unusual between the age groups.

MIS 5a and MIS 7

Table 5.161a, b shows the results from 2-way classification Chi square tests (2x2 contingency tables) for tooth breakage in age groups MIS 5a and 7.

			Broken		
			Broken 1	Unbroken 2	Total
Age group	MIS 5a	Count	15	172	187
		Expected Count	12.1	174.9	187.0
	MIS 7	Count	2	74	76
		Expected Count	4.9	71.1	76.0
Total		Count	17	246	263
		Expected Count	17.0	246.0	263.0

Table 5.161a. Cross-tabulation of age groups (MIS 5a and MIS 7) and tooth breakage for *C. lupus* in Britain. Count and expected count shown. Numbers illustrated used in Chi-square analysis in Table 5.161b.

	Value	df	Asymp. Sig. (2-sided)	Exact Sig. (2-sided)	Exact Sig. (1-sided)
Pearson Chi-Square	2.596[a]	1	.107		
Continuity Correction[b]	1.781	1	.182		
Likelihood Ratio	3.048	1	.081		
Fisher's Exact Test				.165	.085
Linear-by-Linear Association	2.587	1	.108		
N of Valid Cases	263				

Table 5.161b. Results of Chi-square test results for tooth breakage and age groups (MIS 5a and MIS 7) for Britain *C. lupus*. a. 1 cells (25.0%) have expected count less than 5. The minimum expected count is 4.91. Significance indicated by $p<0.05$.

Fisher's Exact test was used as more than 20% of cells have expected counts of <5. Fisher's Exact test was non-significant (FET $p=0.165$), indicating no significant differences in the distribution of tooth breakage. Hence, no association was found between tooth breakage frequency in MIS 5a and MIS 7, with tooth breakage not unusual between these groups.

Summary

MIS 5a contained the highest percentage of broken teeth, with MIS 3 and 7 more similar. However, further analysis using two-way Chi-square tests revealed only MIS 3 and 5a to have significant frequency distributions of tooth breakage.

5.3.8.2. Tooth breakage: *C. lupus* from Europe

All broken teeth were counted and tabulated (Table 5.162) for *C. lupus* from sites on the European mainland.

Site	Site code	Age group	Tot. n teeth	Tot. n broken teeth	% broken teeth	Tot. n unbroken teeth
Grotta di Paglicci	PAG	2	3	1	33.3	2
Tot. Group 2		*2*	*3*	*1*	*33.3*	*2*
Hohlerfels im Achtal	HFA	2.4	2	0	0	0
Perick Cave	PRK	2.4	21	0	0	0
Ranis	RNS	2.4	2	0	0	0
Tot. Group 2.4		*2.4*	*25*	*0*	*0*	*0*
Bad Canstatt, (Villa Seckendorf)	BCT VS	2.8	39	1	2. 6	38
Taubach	TBH	2.8	7	0	0	0
Tot. Group 2.8		*2.8*	*46*	*1*	*2.2*	*45*
Dobelhaldeschacht	DBL	3	5	0	0	0

Weimar-Ehringsdorf	WEHF	3	6	0	0	0
Tot. Group 3		*3*	*11*	*0*	*0*	*0*

Table 5.162. Counts of broken teeth of *C. lupus* from mainland Europe. Total number of teeth, number of broken teeth, percentage broken teeth and number of unbroken teeth shown. Totals for age groups shown in italics.

Only age groups 2 (late Late Pleistocene) and 2.8 (early Late Pleistocene) contain broken teeth. Further analysis of age group 2 is not possible due to low numbers of teeth, a further lack of comparative age groups also prevented further analysis.

5.3.8.3. Tooth breakage: *C. mosbachensis* from Britain

All broken teeth were counted and tabulated (Table 5.163) for *C. mosbachensis* from Britain.

Site	Site code	MIS	n teeth	n broken teeth	% broken teeth	n unbroken
Cudmore Grove	CMG	9	1	0	0	1
Grays Thurrock	GYT	9	4	0	0	4
Tot. MIS 9		*9*	*5*	*0*	*0*	*5*
Boxgrove	BXG	13	60	0	0	60
Sidestrand	SSD	13	5	0	0	5
Westbury-sub-Mendip	WSM	13	64	3	4.7	61
Tot. MIS 13		*13*	*129*	*3*	*2.3*	*126*
East Runton	ERTN	15	2	0	0	2
Overstrand	OVSD	15	1	0	0	1
West Runton	WRTN	17	5	0	0	5
Tot. CfBF			*8*	*0*	*0*	*8*

Table 5.163. Counts of broken teeth of *C. mosbachensis* from Britain. Total number of teeth, number of broken teeth, percentage broken teeth and number of unbroken teeth shown. Totals for age groups shown in italics.

Only the Westbury-sub-Mendip sample contains broken teeth but due to lack of comparative material, further analysis was not possible.

5.3.8.4. Tooth breakage: *C. mosbachensis* from Europe

All broken teeth were counted and tabulated (Table 5.164) for *C. mosbachensis* from mainland Europe.

Site	Site acronym	Age group	Tot. n teeth	Tot. n broken teeth	% broken teeth	Tot. n unbroken teeth

Cengelle II	**CGL**	3.4	8	0	0	8
Heppenloch	**HPN**	3.4	2	0	0	2
Monte Zoppega	**MZP**	3.4	7	2	28.6	5
Tot. Group 3.4		*3.4*	*17*	*2*	*11.8*	*15*
Voigtstedt	**VGT**	3.8	2	0	0	2
Tot. Group 3.8		*3.8*	*2*	*0*	*0*	*2*
Untermassfeld	**UMF**	4	118	6	5.1	112
Viatelle	**VIA**	4	3	0	0	0
Tot. Group 4		*4*	*121*	*6*	*5.0*	*115*

Table 5.164. Counts of broken teeth of *C. mosbachensis* from Europe. Total number of teeth, number of broken teeth, percentage broken teeth and number of unbroken teeth shown. Totals for age groups shown in italics.

Only age groups 3.4 (mid Middle Pleistocene) and 4 (late Early Pleistocene) contain broken teeth, illustrated in Figure 5.95.

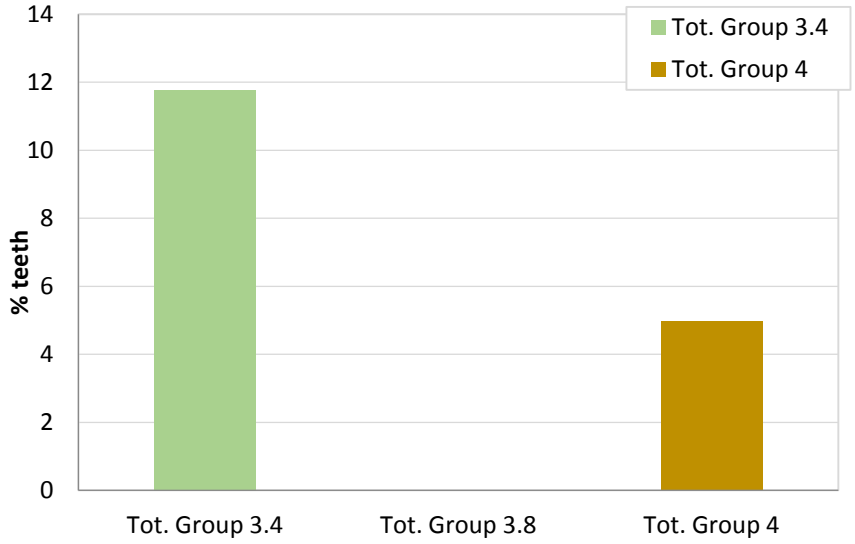


Figure 5.95. Percentage of broken teeth by age group for *C. mosbachensis* from mainland Europe. Age group 4 (late Early Pleistocene), group 3.8 (early Middle Pleistocene), group 3.4 (mid Middle Pleistocene).

Age group 3.8 contains no broken teeth. Out of the age groups, group 3.4 has the highest percentage of broken teeth.

5.3.8.4.1. Statistical analysis of tooth breakage

Table 5.165a, b. shows the results from two-way classification Chi square tests (2x2 contingency tables) for tooth breakage in age groups 3.4 and 4.

			Broken teeth		
			Broken 1	**Unbroken 2**	**Total**
Age group	age group 3.4	Count	2	15	17

		Expected Count	1.0	16.0	17.0
	age group 4	Count	6	112	118
		Expected Count	7.0	111.0	118.0
Total		Count	8	127	135
		Expected Count	8.0	127.0	135.0

Table 5.165a. Cross-tabulation of age groups (3.4 and 4) and tooth breakage for *C. mosbachensis* in Europe. Count and expected count shown. Numbers illustrated used in Chi-square analysis in Table 5.165b.

	Value	df	Asymp. Sig. (2-sided)	Exact Sig. (2-sided)	Exact Sig. (1-sided)
Pearson Chi-Square	1.189[a]	1	.275		
Continuity Correction	.293	1	.588		
Likelihood Ratio	.978	1	.323		
Fisher's Exact Test				.265	.265
Linear-by-Linear Association	1.181	1	.277		
N of Valid Cases	135				

Table 5.165b. Results of Chi-square test for tooth breakage and age groups (3.4 and 4) for *C. mosbachensis* from Europe. a. 1 cells (25.0%) have expected count less than 5. The minimum expected count is 1.01. Significance indicated by $p<0.05$.

As more than 20% of cells have expected counts of <5, Fisher's Exact test was used. Fisher's Exact test was non-significant (FET $p=0.265$), indicating no significant differences were found in the distribution of tooth breakage. Hence, no association was found between tooth breakage frequency in age groups 3.4 and 4.

5.3.8.5. Tooth breakage Europe *C. etruscus*

All broken teeth were counted and tabulated (Table 5.166) for *C. etruscus* from mainland Europe.

Faunal Unit	Site code	Age group	Tot. n teeth	Tot. n broken teeth	% broken teeth	Tot. n unbroken teeth
Upper Valdarno	**UV**	4.4	73	4	5.5	69
Olivola	**OLV**	4.4	39	5	12.8	34
Tot. Group 4.4		*4.4*	*112*	*9*	*8.0*	*103*

Table 5.166. Counts of broken teeth of *C. etruscus* from the European Upper Valdarno and Olivola. Total number of teeth, number of broken teeth, percentage broken teeth and number of unbroken teeth shown. Totals for age groups shown in italics.

Both faunal units of *C. etruscus* contain broken teeth. This is illustrated in Figure 5.96.

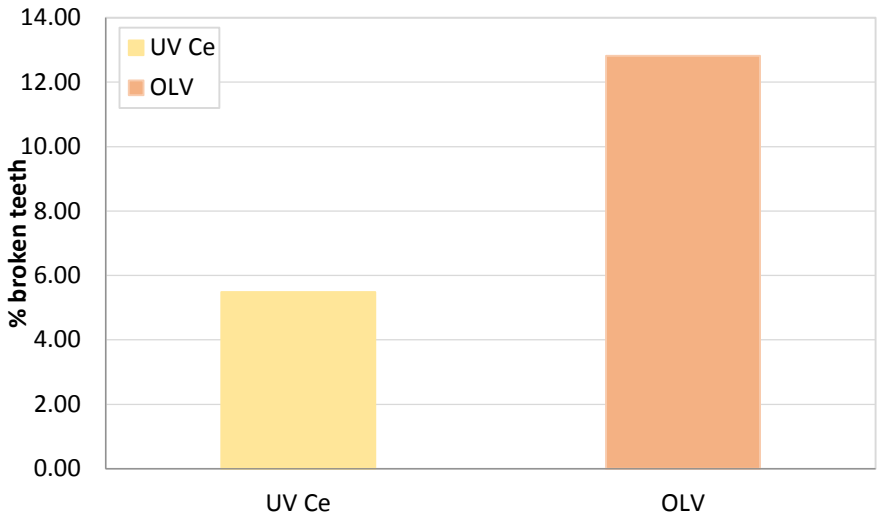


Figure 5.96. Percentage of broken teeth counted in the mid Early Pleistocene age group 4.4, split by Olivola and the Upper Valdarno. Only *C. etruscus* counted.

C. etruscus from Olivola have a higher percentage of tooth breakage than the same species from the slightly younger sites of the Upper Valdarno.

5.3.8.5.1. Statistical analysis of tooth breakage

Table 5.167a, b shows the results of 2-way classification Chi square tests (2x2 contingency tables), for tooth breakage in *C. etruscus* from Olivola and the Upper Valdarno.

			Broken teeth		
			Broken 1	Unbroken 2	Total
Age group	UV	Count	4	69	73
		Expected Count	5.9	67.1	73.0
	OLV	Count	5	34	39
		Expected Count	3.1	35.9	39.0
Total		Count	9	103	112
		Expected Count	9.0	103.0	112.0

Table 5.167a. Cross-tabulation of Olivola and the Upper Valdarno and tooth breakage for *C. etruscus*. Count and expected count shown. Numbers illustrated used in Chi-square analysis in Table 5.167b.

	Value	df	Asymp. Sig. (2-sided)	Exact Sig. (2-sided)	Exact Sig. (1-sided)
Pearson Chi-Square	1.854[a]	1	.173		
Continuity Correction	.993	1	.319		
Likelihood Ratio	1.759	1	.185		
Fisher's Exact Test				.272	.159
Linear-by-Linear Association	1.837	1	.175		
N of Valid Cases	112				

Table 5.167b. Results of chi-square test for tooth breakage and the sites of Olivola and the Upper Valdarno for *C. etruscus*. a. 1 cells (25.0%) have expected count less than 5. The minimum expected count is 3.13. Significance indicated by $p<0.05$.

As more than 20% of cells have expected counts of <5, Fisher's Exact test was used. Fisher's Exact test was non-significant (FET *p*=0.272), indicating no significant differences in the distribution of tooth breakage, and therefore an association between tooth breakage and age group exists.

5.3.8.6. Tooth breakage analysis: *C. arnensis* from Europe

All broken teeth were counted and tabulated (Table 5.168) for *C. arnensis* from the Upper Valdarno.

Site	Site code	Age	Tot. n teeth	Tot. n broken teeth	% broken teeth	Tot. n unbroken teeth
Upper Valdarno	**UV Ca**	4.4	81	1	1.2	80
Tot. Group 4.4		*4.4*	*81*	*1*	*1.2*	*80*

Table 5.168. Counts of broken teeth of *C. arnensis* from the Upper Valdarno. Total number of teeth, number of broken teeth, percentage broken teeth and number of unbroken teeth shown. Totals for age groups shown in italics.

A single tooth was counted as broken for *C. arnensis* from the Upper Valdarno. Further analysis was not possible due to no comparative material. When compared to sympatric *C. etruscus*, *C. arnensis* had a lower number of broken teeth. Figure 5.97 compares tooth breakage between *C. etruscus* and *C. arnensis* from the Upper Valdarno.

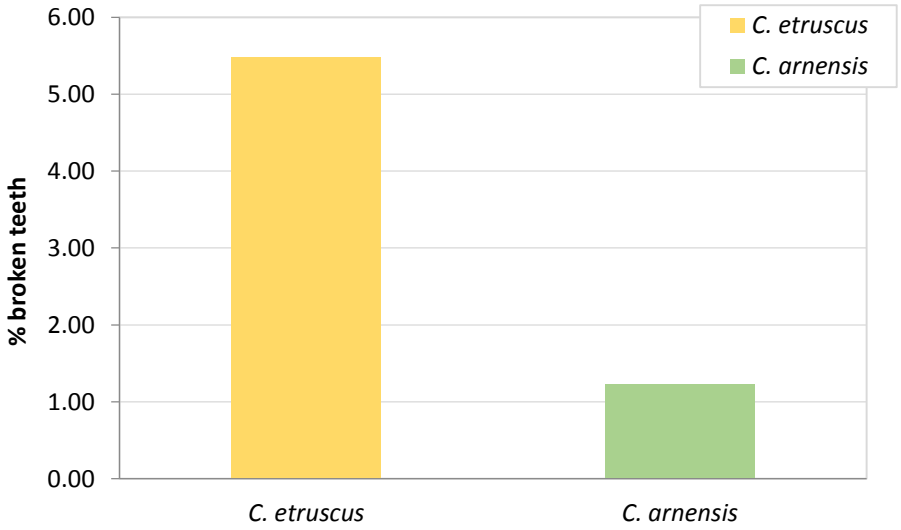


Figure 5.97. Comparison of the percentage of tooth breakage present in *C. etruscus* and *C. arnensis* from the Upper Valdarno.

As illustrated, *C. etruscus* had higher incidences of broken teeth than *C. arnensis*, although both percentages are low in number in comparison to *C. lupus*.

Summary

Variation in the percentage of broken teeth was present in all species. From Chi-square analysis of tooth breakage frequencies, only *C. lupus* from MIS 3 and 5a in Britain was significant, indicating that tooth breakage frequency between these age groups was related to temporal differences. It is of note that the frequency of breakage between MIS 3 and 7, and MIS 5a and 7 was non-significant in comparison.

Not enough data were present for further analysis of *C. lupus* or *C. arnensis* from mainland Europe, or *C. mosbachensis* from Britain. Further analysis of *C. mosbachensis* from Europe revealed tooth breakage frequencies as non-significant, as did the analysis of *C. etruscus* from Olivola and the Upper Valdarno.

5.3.9. Tooth wear

Tooth wear was assigned a wear score (W1-5) indicating slight, moderate or heavy wear. Analysis of tooth wear was carried out on *C. lupus* from Pleistocene Britain and Europe, as well as for *C. mosbachensis, C. etruscus and C. arnensis*.

5.3.9.1. Tooth wear analysis: *C. lupus* from Britain

All worn teeth were counted and tabulated (Table 5.169) for *C. lupus* from Britain. Both MIS 5a and 6 are typified by high numbers of heavily worn teeth, whilst in contrast MIS 5e and 7 have the lowest numbers of heavily worn teeth. Figure 5.98 summarises the percentages of worn teeth by wear category in the *C. lupus* age groups from Britain.

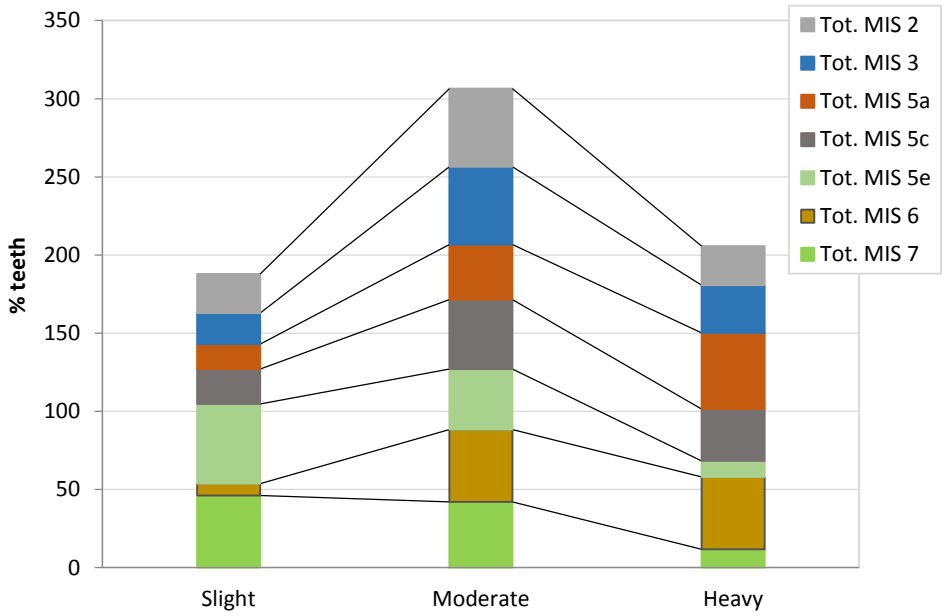


Figure 5.98. Summary of the percentages of worn teeth by wear category in *C. lupus* age groups from Britain.

MIS 5e and 7 have the highest percentages of slightly worn teeth, and low percentages of heavily worn teeth. In contrast, MIS 5a and 6 have the highest percentages of heavily worn teeth, and low percentages of slightly worn teeth. Both MIS 2 and 3 have similarly equal distributions of tooth wear in each category.

Some of the age groups however contain low numbers of teeth from few sites (e.g. MIS 2, 5c, 5e and 6), making further inferences on the distribution of wear difficult. Henceforth, MIS 3, 5a and 7 will be focussed on, due to containing higher numbers of teeth.

Site	Site code	MIS	Tot. n teeth	n teeth & % with wear score						Tot. n broken
				Slight	%	Moderate	%	Heavy	%	
Cae Gywn Cave	**CGC**	2	5	0	0	3	60	2	40	0
Ogof yr Ychen	**OGF**	2	7	3	42.9	3	42.9	1	14.3	0
Tot. MIS 2		*2*	*12*	*3*	*25.0*	*6*	*50.0*	*3*	*25.0*	*0*
Black Rock Quarry	**BRQ**	3	23	5	21.7	7	30.4	11	47.8	0
Kents Cavern (Cave Earth)	**KC**	3	24	4	16.7	10	41.7	10	41.7	1
Oreston Cave	**OSTN**	3	44	14	31.8	22	50.0	8	18.2	2
Paviland	**PAV**	3	32	5	15.6	18	56.3	9	28.1	1
Pin Hole Cave	**PHC**	3	32	3	9.4	18	56.3	11	34.4	0
Sandford Hill	**SFH**	3	4	0	0	4	100.0	0	0	0
Uphill Cave	**UPH**	3	2	1	50.0	1	50.0	0	0	0
Tot. MIS 3		*3*	*161*	*32*	*19.9*	*80*	*49.7*	*49*	*30.4*	*4*
Banwell Bone Cave	**BWL**	5a	125	11	8.8	47	37.6	67	53.6	12
Bosco's Den	**BSD**	5a	23	6	26.1	9	39.1	8	34.8	2
Steetley Quarry	**STQ**	5a	4	0	0	2	50.0	2	50.0	0
Stump Cross Cave	**SCC**	5a	8	8	100.0	0	0	0	0	0
Windy Knoll	**WK**	5a	19	5	26.3	8	42.1	6	31.6	1
Wretton	**WTN**	5a	8	0	0	0	0	8	100.0	0
Tot. MIS 5a		*5a*	*187*	*30*	*16.0*	*66*	*35.3*	*91*	*48.7*	*15*
Bacon Hole	**BH**	5c	5	1	20.0	1	20.0	3	60.0	1
Minchin Hole	**MCN**	5c	2	0	0	2	100.0	0	0	1
Pickens Hole (Layer 5)	**PKN**	5c	2	1	50.0	1	50.0	0	0	0
Tot. MIS 5c		*5c*	*9*	*2*	*22.2*	*4*	*44.4*	*3*	*33.3*	*2*
Barrington	**BTN**	5e	2	0	0	2	100.0	0	0	1

Joint Mitnor Cave	**JMC**	5e	47	25	53.2	17	36.2	5	10.6	1
Tot. MIS 5e		*5e*	*49*	*25*	*51.0*	*19*	*38.8*	*5*	*10.2*	*2*
Clevedon Cave	**CVD**	6	39	3	7.7	18	46.2	18	46.2	3
Tot. MIS 6		*6*	*39*	*3*	*7.7*	*18*	*46.2*	*18*	*46.2*	*3*
Crayford	**CYD**	7	7	1	14.3	5	71.4	1	14.3	1
Hutton Cave	**HTN**	7	28	10	35.7	17	60.7	1	3.6	1
Ilford	**ILF**	7	5	4	80.0	1	20.0	0	0	0
Marsworth	**MRSW**	7	9	7	77.8	1	11.1	1	11.1	0
Pontnewydd Cave (L. Breccia & Int. Layer)	**PNC**	7	24	10	41.7	8	33.3	6	25.0	0
Tornewton Cave Otter Stratum	**TNC OS**	7	3	3	100.0	0	0.0	0	0.0	0
Tot. MIS 7		*7*	*76*	*35*	*46.1*	*32*	*42.1*	*9*	*11.8*	*2*

Table 5.169. Tooth wear and breakage data for *C. lupus* from Britain. Total number of teeth shown. Number of teeth assigned to wear category shown as counts and percentages. Rows in italics indicate the total number of teeth for each MIS age assigned to wear score also shown as total counts and percentages. Number of teeth identified as broken shown.

Figure 5.99 summarises the distribution of tooth wear for MIS 3, 5a and 7.

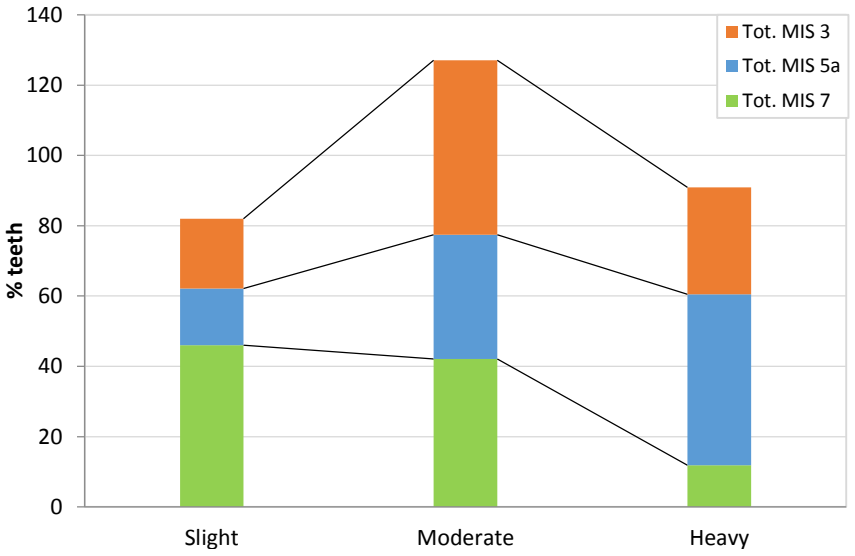


Figure 5.99. Summary of the percentages of worn teeth by wear category for MIS 3, 5a and 7.

MIS 7 contains the highest percentages of slight wear, and lowest percentage of heavily worn teeth. In contrast, tooth wear at MIS 5a contains the highest percentage of heavily worn teeth. MIS 3 contains the highest percentage of moderately worn teeth, with a more balanced distribution of slight and heavily worn teeth.

Figure 5.100 illustrates the percentages of worn teeth present in sites of MIS 3 age for *C. lupus*.

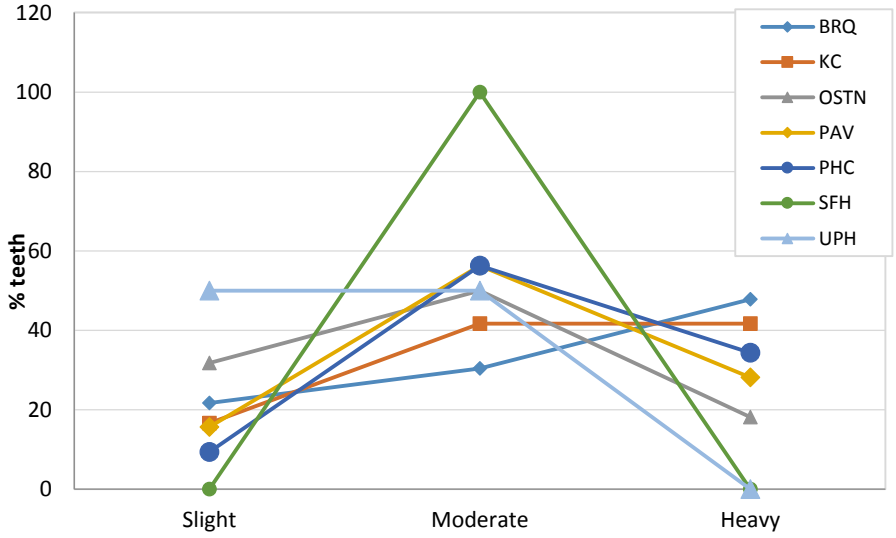


Figure 5.100. Percentages of worn teeth by wear category in sites of MIS 3 age in Britain. Site codes listed in Table 5.169.

Moderate tooth wear is consistently high in all analysed sites of MIS 3. Black Rock Quarry, Kents Cavern, Paviland and Pin Hole Cave all have high percentages of heavily worn teeth, whilst Oreston Cave and Uphill both have more slightly worn teeth. Sandford Hill is anomalous due to the low amount of teeth present.

Figure 5.101 illustrates the percentages of worn teeth by wear category in sites of MIS 5a age.

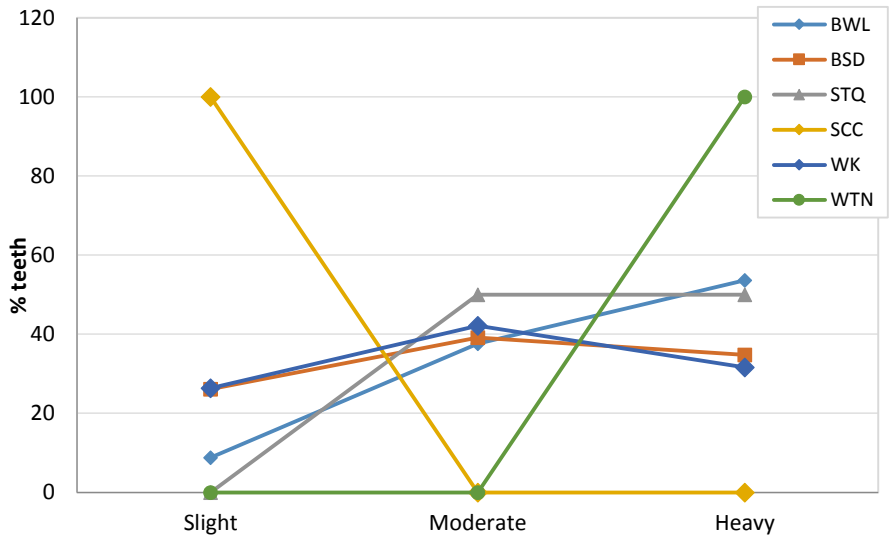


Figure 5.101. Percentages of worn teeth by wear category in sites of MIS 5a in Britain. Site codes listed in Table 5.169.

The distribution of wear for analysed sites of MIS 5a indicates higher percentages of heavily worn teeth with much lower percentages of slightly worn teeth. Banwell Bone Cave and Steetley Quarry contain the highest percentage of heavily worn teeth. Both Bosco's Den and Windy Knoll both have similar distributions of tooth wear, with more moderately and heavily worn teeth. Both Stump Cross Cave and Wretton are anomalous due to low numbers of teeth.

Figure 5.102 illustrates the percentages of worn teeth by wear category in sites of MIS 7 age.

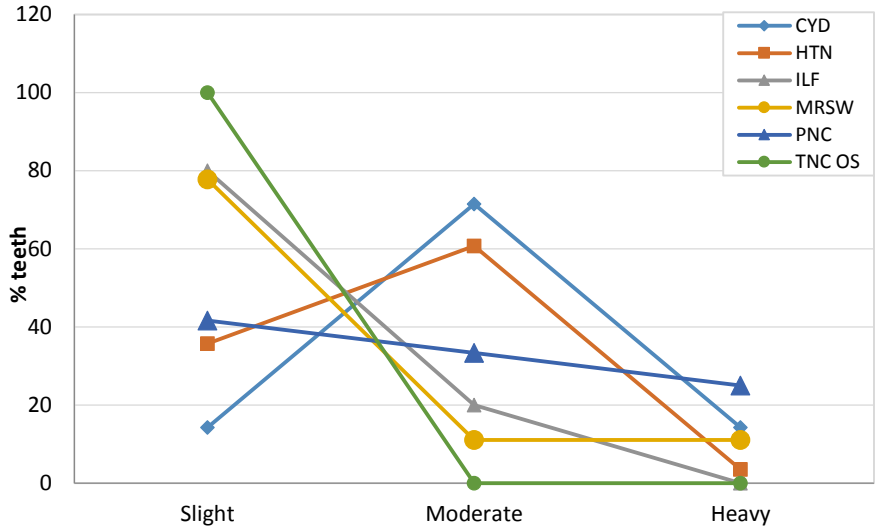


Figure 5.102. Percentages of worn teeth by wear category in sites of MIS 7 in Britain. Site codes listed in Table 5.169.

Sites of MIS 7 contain high percentages of slightly and moderately worn teeth, with lower percentages of heavily worn teeth. Ilford, Marsworth, Pontnewydd Cave and Tornewton Cave (Otter Stratum) have the highest percentages of slightly worn teeth. Both Hutton Cave and Crayford have high percentages of moderately worn teeth.

5.3.9.1.1. Statistical analysis of tooth wear

Two-way classification Chi square tests (using 2x3 contingency tables) were used to determine whether the differences between the frequencies of tooth wear were related to temporal differences.

MIS 3 and MIS 5a

Table 5.170a, b shows the results from two-way classification Chi square tests (using 2x3 contingency tables) for tooth wear in MIS 3 and 5a.

			Wear			
			Slight wear 1	Moderate wear 2	Heavy wear 3	Total
Age	MIS 3	Count	32	80	49	161
		Expected Count	28.7	67.5	64.8	161.0
	MIS 5a	Count	30	66	91	187
		Expected Count	33.3	78.5	75.2	187.0
Total		Count	62	146	140	348
		Expected Count	62.0	146.0	140.0	348.0

Table 5.170a. Cross-tabulation of counts and expected counts of numbers of teeth in tooth wear categories (slight (1), moderate (2), heavy (3)) for MIS 3 and 5a containing *C. lupus* from Britain. Numbers illustrated used in Chi-square analysis in Table 5.170b.

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	12.132[a]	2	.002
Likelihood Ratio	12.261	2	.002
Linear-by-Linear Association	7.919	1	.005
N of Valid Cases	348		

Table 5.170b. Results of Chi-square test for wear categories and age groups MIS 3 and 5a for British *C. lupus*. a. 0 cells (.0%) have expected count less than 5. The minimum expected count is 28.68. Significance indicated by $p<0.05$.

The Pearson Chi-square for tooth wear in MIS 3 and 5a was significant ($\chi^2= 12.132$, $N = 348$, $p=0.002$), indicating differences in the distribution of tooth wear, and hence an association between tooth wear frequency and age group exists.

MIS 3 and MIS 7

Table 5.171a, b shows the results from two-way classification Chi square tests (using 2x3 contingency tables) for tooth wear in MIS 3 and 7.

			Wear			
			Slight wear 1	Moderate wear 2	Heavy wear 3	Total
Age	MIS 3	Count	32	80	49	161
		Expected Count	45.5	76.1	39.4	161.0
	MIS 7	Count	35	32	9	76
		Expected Count	21.5	35.9	18.6	76.0
Total		Count	67	112	58	237
		Expected Count	67.0	112.0	58.0	237.0

Table 5.171a. Cross-tabulation of counts and expected counts of numbers of teeth in tooth wear categories (slight (1), moderate (2), heavy (3)) for MIS 3 and 7 containing *C. lupus* from Britain. Numbers illustrated used in Chi-square analysis in Table 5.171b.

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	20.435[a]	2	.0001
Likelihood Ratio	20.554	2	.0001
Linear-by-Linear Association	19.591	1	.0001
N of Valid Cases	237		

Table 5.171b. Results of Chi-square test for wear categories and age groups MIS 3 and 7 for British *C. lupus*. a. 0 cells (.0%) have expected count less than 5. The minimum expected count is 18.60. Significance indicated by $p<0.05$.

The Pearson Chi-square for tooth wear in MIS 3 and 7 was significant ($\chi^2= 20.435$, $N = 237$, $p=0.0001$), indicating differences in the distribution of tooth wear. Thus, an association exists in the wear frequencies between MIS 3 and 7.

MIS 5a and MIS 7

Table 5.172a, b shows the results from two-way classification Chi square tests (using 2x3 contingency tables) for tooth wear in MIS 5a and 7.

			Wear			
			Slight wear 1	Moderate wear 2	Heavy wear 3	Total
Age	MIS 5a	Count	30	66	91	187
		Expected Count	46.2	69.7	71.1	187.0
	MIS 7	Count	35	32	9	76
		Expected Count	18.8	28.3	28.9	76.0
Total		Count	65	98	100	263
		Expected Count	65.0	98.0	100.0	263.0

Table 5.172a. Cross-tabulation of counts and expected counts of numbers of teeth in tooth wear categories (slight (1), moderate (2), heavy (3)) for MIS 5a and 7 containing *C. lupus* from Britain. Numbers illustrated used in Chi-square analysis in Table 5.172b.

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	39.632[a]	2	.0001
Likelihood Ratio	42.203	2	.0001
Linear-by-Linear Association	39.437	1	.0001
N of Valid Cases	263		

Table 5.172b. Results from Chi-square test for wear categories and age groups MIS 5a and 7 for British *C. lupus*. a. 0 cells (.0%) have expected count less than 5. The minimum expected count is 18.78. Significance indicated by $p<0.05$.

The Pearson Chi-square for tooth wear in MIS 5a and 7 was significant ($\chi^2= 39.632$, $N = 263$, $p=0.0001$), indicating differences in the distribution of tooth wear, and thus an association in the wear frequencies between MIS 5a and 7 is present.

5.3.9.2. Tooth wear analysis: *C. lupus* from Europe

All worn teeth were counted and tabulated (Table 5.173) for *C. lupus* from mainland Europe. Age groups 2.4 and 2.8 (mid and early Late Pleistocene) contain the highest percentages of heavy wear. Figure 5.103 summarises the percentages of worn teeth by wear category in the *C. lupus* age groups.

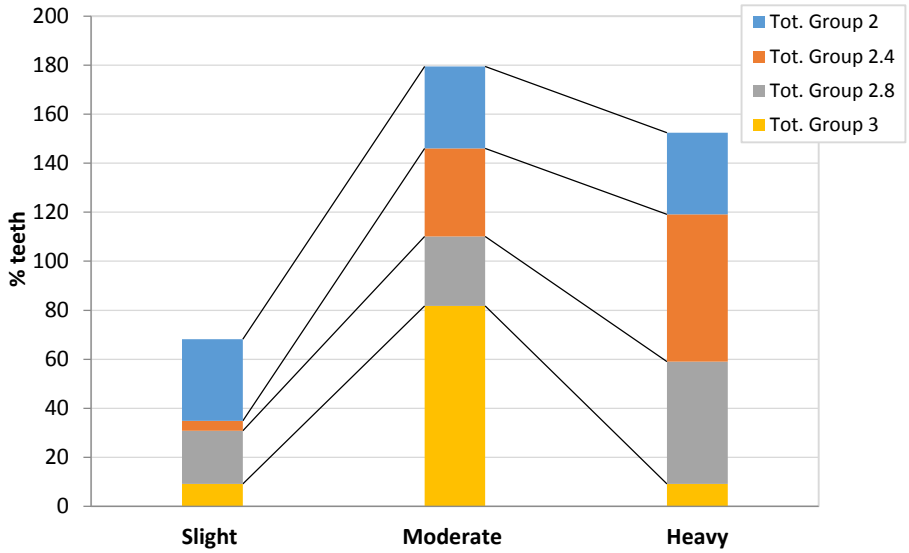


Figure 5.103. Summary of the percentages of worn teeth by wear category in *C. lupus* age groups of the late Middle (group 3), early Late Pleistocene (group 2.8), mid Late Pleistocene (group 2.4) and late Late Pleistocene (group 2).

Age groups 2.4 and 2.8 contain the highest percentages of heavily worn teeth, with group 2.4 also having low percentages of slightly worn teeth. Group 2.8 has similar amounts of slightly and moderately worn teeth. Age group 3 contains the highest amount of moderately worn teeth. Further analysis will focus on age groups 2.4 and 2.8, as groups 2 and 3 contained low numbers of teeth. Figure 5.104 illustrates the percentages of worn teeth in sites of age group 2.4.

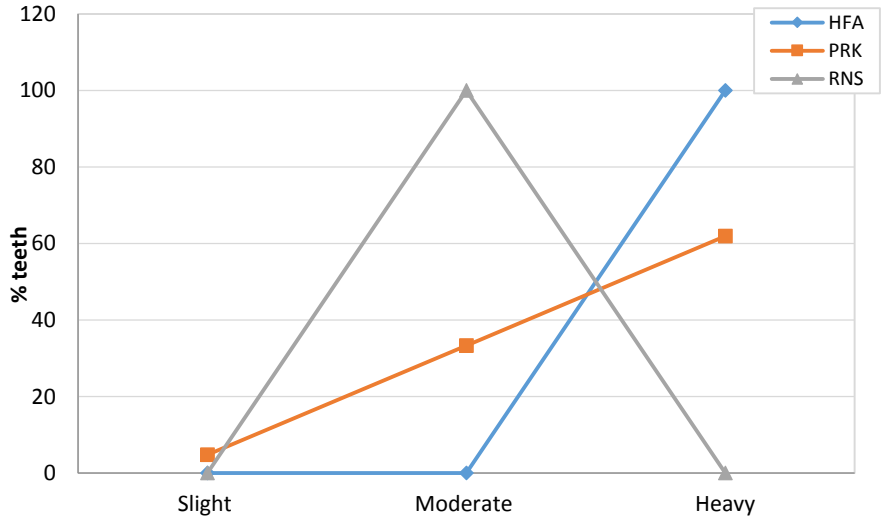


Figure 5.104. Percentages of worn teeth by wear category in sites of age group 2.4 (mid Late Pleistocene) in Europe. Site codes in Table 5.173.

Site	Site code	Age group	Tot. n teeth	n teeth & % teeth with wear category						n broken teeth
				Slight	%	Moderate	%	Heavy	%	
Grotta Paglicci	PAG	2	3	1	33.3	1	33.3	1	33.3	1
Tot. Group 2		*2*	*3*	*1*	*33.3*	*1*	*33.3*	*1*	*33.3*	*1*
Hohlerfels im Achtal	HFA	2.4	2	0	0	0	0	2	100.0	0
Perick Cave	PRK	2.4	21	1	4.8	7	33.3	13	61.9	0
Ranis	RNS	2.4	2	0	0	2	100.0	0	0	0
Tot. Group 2.4		*2.4*	*25*	*1*	*4.0*	*9*	*36.0*	*15*	*60.0*	*0*
Bad Canstatt, Villa Seckendorf	BCT VS	2.8	39	9	23.1	9	23.1	21	53.9	1
Taubach	TBH	2.8	7	1	14.3	4	57.1	2	28.6	0
Tot. Group 2.8		*2.8*	*46*	*10*	*21.7*	*13*	*28.3*	*23*	*50.0*	*1*
Dobelhaldeschacht	DBL	3	5	1	20.0	4	80.0	0	0	0
Weimar-Ehringsdorf	WEHF	3	6	0	0	5	83.3	1	16.7	0
Tot. Group 3		*3*	*11*	*1*	*9.1*	*9*	*81.8*	*1*	*9.1*	*0*

Table 5.173. Tooth wear and breakage data for *C. lupus* from Europe. Total number of teeth shown. Number of teeth assigned to wear category shown as counts and percentages. Rows in italics indicate the total number of teeth for each age group assigned to wear category also shown as total counts and percentages. Number of teeth identified as broken shown.

Perick Cave had the highest percentage of heavily worn teeth, with few slightly worn teeth. The low numbers of teeth counted at Hohle Fels and Ranis (Table 5.173) reflect less reliable tooth wear distributions.

Figure 5.105 illustrates the percentages of worn teeth present in sites of age group 2.8 (early Late Pleistocene).

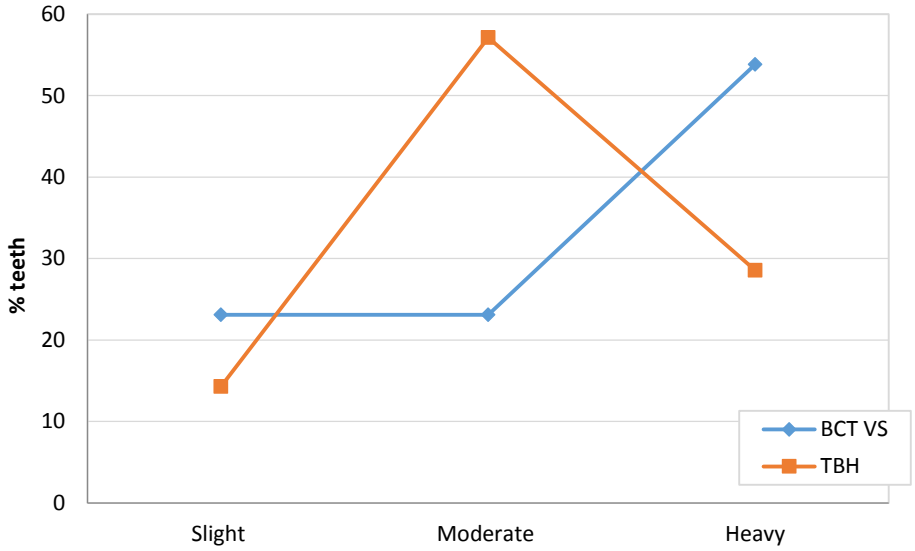


Figure 5.105. Percentages of worn teeth by wear category in sites of age group 2.8 (early Late Pleistocene) in Europe. Site codes in Table 5.173.

Bad Canstatt (Villa Seckendorff) contains the highest number of teeth in the age group and has the highest percentage of heavily worn teeth. Taubach contains fewer teeth, albeit of predominantly moderate wear.

5.3.9.2.1. Statistical analysis of tooth wear

As with the analysis of tooth wear in Britain for *C. lupus*, two-way classification Chi square tests (using 2x3 contingency tables) were used to assess tooth wear frequency.

Age groups 2.4 and 2.8 (early Late and mid Late Pleistocene)

Table 5.174a, b. shows the results from two-way classification Chi square tests (using 2x3 contingency tables) for tooth wear in age groups 2.4 and 2.8.

			Wear			
			Slight	Moderate	Heavy	Total
Age group	Age group 2.4	Count	1	10	16	27
		Expected Count	4.1	8.5	14.4	27.0

Age group 2.8	Count	10	13	23	46
	Expected Count	6.9	14.5	24.6	46.0
Total	Count	11	23	39	73
	Expected Count	11.0	23.0	39.0	73.0

Table 5.174a. Cross-tabulation of counts and expected counts of numbers of teeth in tooth wear categories (slight (1), moderate (2), heavy (3)) for age groups 2.4 and 2.8 containing *C. lupus* from Europe. Numbers illustrated used in Chi-square analysis in Table 5.174b.

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	4.362[a]	2	.113
Likelihood Ratio	5.200	2	.074
Linear-by-Linear Association	2.325	1	.127
N of Valid Cases	73		

Table 5.174b. Results from Chi-square test of wear categories and age groups 2.4 and 2.8 for Europe *C. lupus*. a. 1 cells (16.7%) have expected count less than 5. The minimum expected count is 4.07. Significance indicated by $p<0.05$.

One cell was found to have an expected count of <5, yet since this represents less than 20% of the cells in total, the Pearson Chi-square result will be used. The Pearson Chi-square test was non-significant ($\chi^2= 4.362$, $N =73$, $p=0.113$), indicating no differences in the distribution of tooth wear, and no association between the wear and age groups.

5.3.9.3. Tooth wear analysis: *C. mosbachensis* from Britain

All worn teeth were counted and tabulated (Table 5.175) for *C. mosbachensis* from Britain. In comparison to *C. lupus* in Britain, *C. mosbachensis* has higher percentages of slightly worn teeth across all age groups, with significantly less heavily worn teeth.

Site	Site code	MIS	n teeth	n teeth & % teeth with wear score						n broken teeth
				Slight	%	Moderate	%	Heavy	%	
Cudmore Grove	CMG	9	1	0	0	0	0	1	100.0	0
Grays Thurrock	GYT	9	4	1	25.0	3	75.0	0	0	0
Tot. MIS 9		*9*	*5*	*1*	*20.0*	*3*	*60.0*	*1*	*20.0*	*0*
Boxgrove	BXG	13	60	36	60.0	24	40.0	0	0	0
Sidestrand	SSD	13	5	0	0	3	60.0	2	40.0	0
Westbury-sub-Mendip	WSM	13	64	34	53.1	22	34.4	8	12.5	3
Tot. MIS 13		*13*	*129*	*70*	*54.3*	*49*	*38.0*	*10*	*7.8*	*3*
East Runton	ERTN	15	2	1	50.0	1	50.0	0	0	0
Overstrand	OVSD	15	1	1	100.0	0	0	0	0	0
West Runton	WRTN	17	5	2	40.0	3	60.0	0	0	0
Tot. CfBF		*CfBF*	*8*	*4*	*50.0*	*4*	*50.0*	*0*	*0*	*0*

Table 5.175. Tooth wear and breakage data for *C. mosbachensis* from Britain. Total number of teeth shown. Number of teeth assigned to wear category shown as counts and percentages. Rows in italics indicate the total number of teeth for each age group assigned to wear category also shown as total counts and percentages. Number of teeth identified as broken shown.

Figure 5.106 summarises the percentages of worn teeth by wear category in the *C. mosbachensis* age groups from Britain.

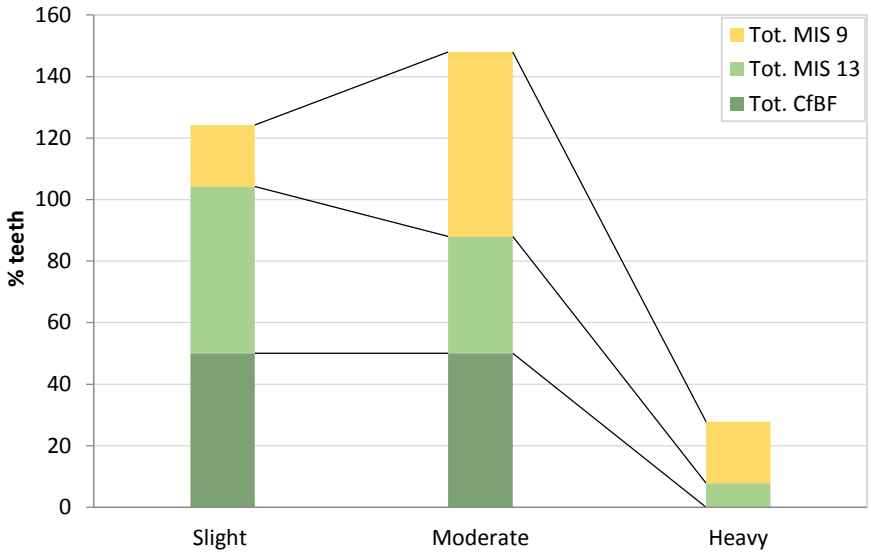


Figure 5.106. Summary of the percentages of worn teeth by wear category in *C. mosbachensis* age groups from Britain.

MIS 9 contains the highest percentage of moderately worn teeth. In contrast, MIS 13 contains higher percentages of slightly worn teeth, combined with low percentages of heavily worn teeth. Members of the Cromer Forest-bed Formation also contain high percentages of slight and moderately worn teeth, with none that are heavily worn.

The MIS 13 group contains the highest number of teeth, split between Boxgrove and Westbury-sub-Mendip. These sites will be further analysed. The remaining age groups contain too few numbers to make reliable inferences on tooth wear distributions.

Figure 5.107 shows the percentages of teeth with wear by site for MIS 13.

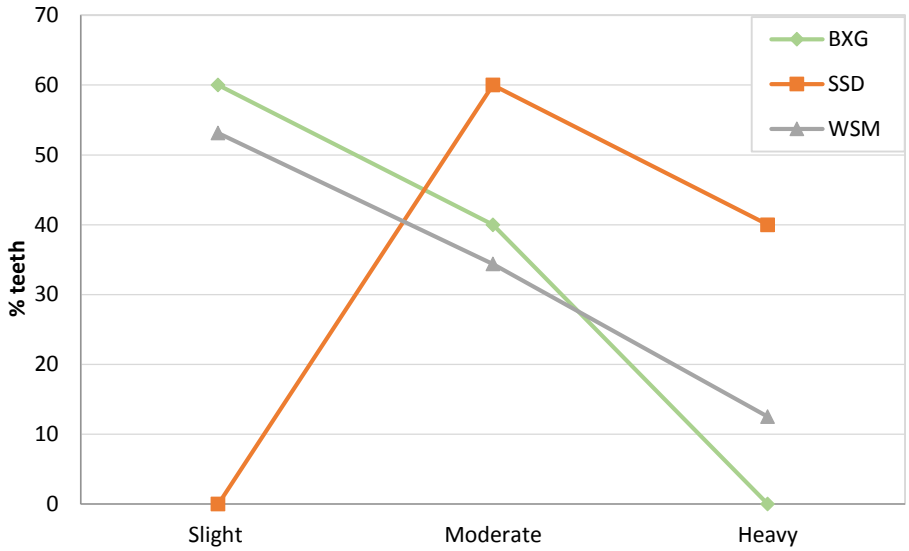


Figure 5.107. Percentages of worn teeth by wear category in sites of MIS 13 in Britain. See Table 5.175 for site codes.

Both Boxgrove and Westbury-sub-Mendip have similar distributions of tooth wear, with high percentages of slightly worn teeth, and low percentages of heavily worn teeth. Sidestrand is represented by few individuals in comparison, and thus the distribution of tooth wear may not be a reliable reflection of wear in this population.

5.3.9.3.1. Statistical analysis of tooth wear

Table 5.176a, b. shows the results from two-way classification Chi square tests (using 2x3 contingency tables) examining the differences in frequencies of tooth wear temporally between the combined similarly aged (MIS 13) sites of Boxgrove and Sidestrand, and Westbury-sub-Mendip.

			Wear			
			Slight	Moderate	Heavy	Total
Age	BXG+SSD	Count	36	27	2	65
		Expected Count	35.3	24.7	5.0	65.0
	WSM	Count	34	22	8	64
		Expected Count	34.7	24.3	5.0	64.0
Total		Count	70	49	10	129
		Expected Count	70.0	49.0	10.0	129.0

Table 5.176a. Cross-tabulation of counts and expected counts of numbers of teeth in tooth wear categories (slight (1), moderate (2), heavy (3)) for temporally different sites of Boxgrove/Sidestrand and Westbury-sub-Mendip containing *C. mosbachensis* from Britain. Numbers illustrated used in Chi-square analysis in Table 5.176b.

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	4.160[a]	2	.125

Likelihood Ratio	4.415	2	.110
Linear-by-Linear Association	1.081	1	.298
N of Valid Cases	129		

Table 5.176b. Results from Chi-square test between wear categories and temporally different sites of Boxgrove/Sidestrand and Westbury-sub-Mendip containing *C. mosbachensis* from Britain. a. 1 cells (16.7%) have expected count less than 5. The minimum expected count is 4.96. Significance indicated by $p<0.05$.

One cell has an expected count of <5, however, as it represents less than 20% of the total cells, the Pearson Chi-square result will be used. The Pearson Chi-square test was non-significant ($\chi^2=4.160$, $N=129$, $p=0.125$), indicating no differences in the distribution of tooth wear, and no association between tooth wear and the sites of Boxgrove/Sidestrand and Westbury-sub-Mendip.

5.3.9.4. Tooth wear analysis: *C. mosbachensis* from mainland Europe

All worn teeth were counted and tabulated (Table 5.177) for *C. mosbachensis* from Europe. Moderate tooth wear accounted for the highest percentages of teeth at all sites. Figure 5.109 illustrates the percentages of worn teeth in age groups 4, 3.8 and 3.4 (late Early Pleistocene to the mid Middle Pleistocene).

Site	Site code	Age group	Total n teeth	n teeth & % teeth with wear score						n broken teeth
				Slight	%	Moderate	%	Heavy	%	
Cengelle II	**CGL**	3.4	8	3	37.5	5	62.5	0	0	0
Heppenloch	**HPN**	3.4	2	2	100.0	0	0	0	0	0
Monte Zoppega	**MZP**	3.4	7	0	0	4	57.1	3	42.9	2
Tot. Group 3.4		*3.4*	*17*	*5*	*29.4*	*9*	*52.9*	*3*	*17.7*	*2*
Voigtstedt	**VGT**	3.8	2	0	0	1	50.0	1	50.0	0
Tot. Group 3.8		*3.8*	*2*	*0*	*0*	*1*	*50.0*	*1*	*50.0*	*0*
Untermassfeld	**UMF**	4	118	30	25.4	52	44.1	36	30.5	6
Viatelle	**VIA**	4	3	2	66.7	1	33.3	0	0	0
Tot. Group 4		*4*	*121*	*32*	*26.5*	*53*	*43.8*	*36*	*29.8*	*6*

Table 5.177. Tooth wear and breakage data for *C. mosbachensis* from Europe. Total number of teeth shown. Number of teeth assigned to wear category shown as counts and percentages. Rows in italics indicate the total number of teeth for each age group assigned to wear category also shown as total counts and percentages. Number of teeth identified as broken shown.

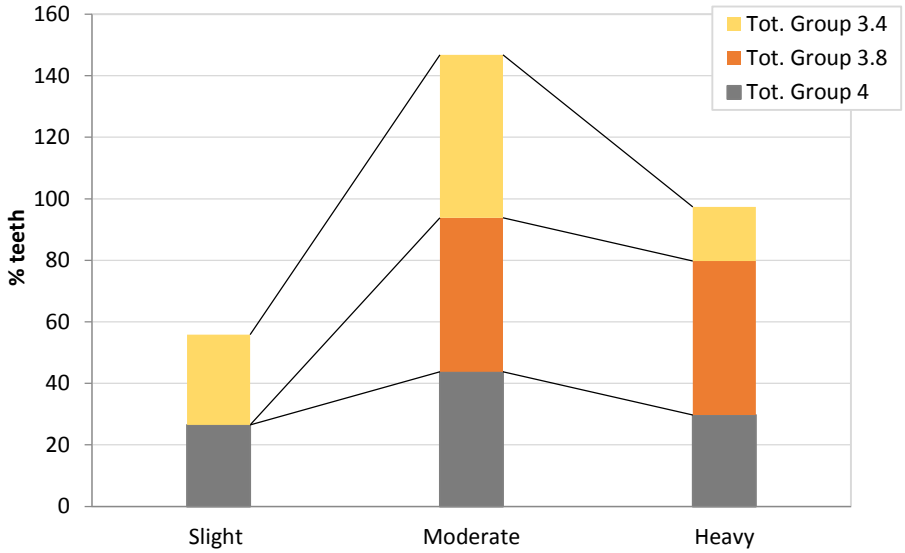


Figure 5.108. Summary of the percentages of worn teeth by wear category in *C. mosbachensis* age groups. Age group 4 (late Early Pleistocene), 3.8 (early Middle Pleistocene), 3.4 (mid Middle Pleistocene).

Age group 4 has a high percentage of moderately worn teeth, combined with more equal proportions of slightly and heavily worn teeth, similar to age group 3.4. Age group 3.8 contains equal numbers of moderate to heavily worn teeth.

Age group 4 (late Early Pleistocene) contains the highest numbers of teeth. Figure 5.109 illustrates the percentage of worn teeth with wear for the sites comprising age group 4.

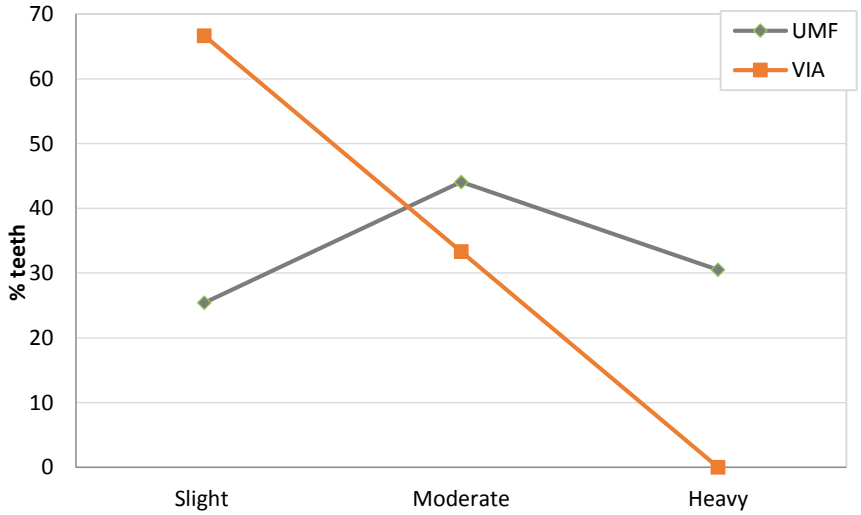


Figure 5.109. Percentages of worn teeth by wear category in sites of age group 4 (late Early Pleistocene) in Europe. Sites codes listed in Table 5.177.

The distribution of wear at Viatelle may be anomalous due to very low numbers of teeth counted (Table 5.117). At Untermassfeld, moderate tooth wear represents the highest

percentage, with slight and heavy wear more similar. Further statistical analysis was not possible due to the lack of teeth in comparable European sites.

Nonetheless, the tooth wear data from Untermassfeld was compared to the British sites of MIS 13 age also containing *C. mosbachensis*. Figure 5.110 compares the percentages of worn teeth for these age groups.

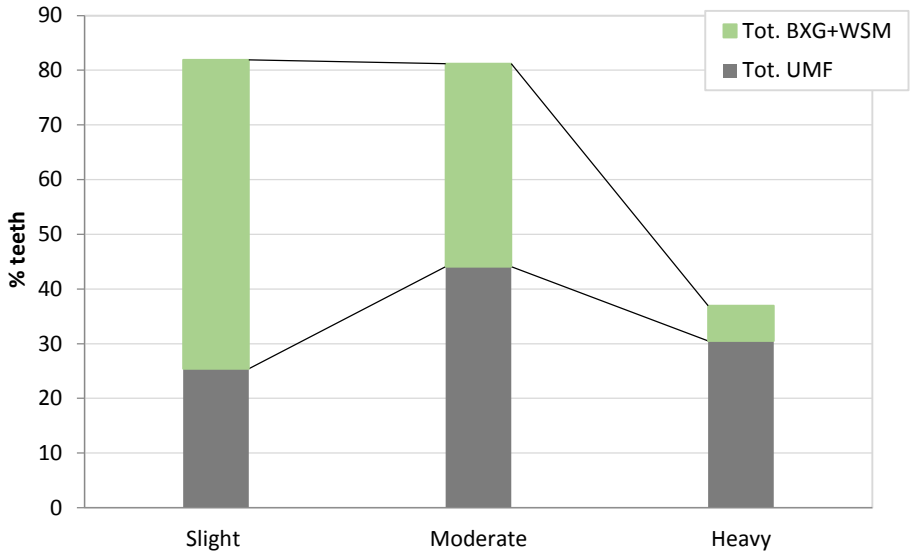


Figure 5.110. Summary of the percentages of worn teeth by wear category in *C. mosbachensis* from MIS 13 in Britain and the late Early Pleistocene age group (group 4) of Untermassfeld.

In comparison to the older age group 4, the distribution of tooth wear during MIS 13 is skewed more towards slight wear, with comparatively lower percentages of moderately and heavily worn teeth. This is in contrast to age group 4, which has a higher percentage of moderately worn teeth, and more similar percentages of slight and heavily worn teeth.

5.3.9.4.1. Statistical analysis of tooth wear

Tables 5.178a, b. shows the results of two-way classification Chi square tests (using 2x3 contingency tables) for *C. mosbachensis* from Untermassfeld (age group 4, late Early Pleistocene) and MIS 13 sites of Boxgrove, Sidestrand and Westbury-sub-Mendip.

			Wear			
			Slight	**Moderate**	**Heavy**	**Total**
Age	UMF	Count	30	52	36	118
		Expected Count	47.8	48.3	22.0	118.0
	BXG, SSD, WSM	Count	70	49	10	129
		Expected Count	52.2	52.7	24.0	129.0
Total		Count	100	101	46	247

Expected Count	100.0	101.0	46.0	247.0

Table 5.178a. Cross-tabulation of counts and expected counts of numbers of teeth in tooth wear categories (slight (1), moderate (2), heavy (3)) for MIS 13 (Boxgrove, Sidestrand, Westbury-sub-Mendip) and age group 4 (Untermassfeld) containing *C. mosbachensis*. Numbers illustrated used in Chi-square analysis in Table 5.178b.

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	30.355[a]	2	.0001
Likelihood Ratio	31.655	2	.0001
Linear-by-Linear Association	30.076	1	.0001
N of Valid Cases	247		

Table 5.178b. Results from chi-square test of wear categories between MIS 13 (Boxgrove, Sidestrand and Westbury-sub-Mendip) and age group 4 (Untermassfeld) containing *C. mosbachensis*. a. 0 cells (.0%) have expected count less than 5. The minimum expected count is 21.98. Significance indicated by $p<0.05$.

The Pearson Chi-square test for the frequency distribution of tooth wear in MIS 13 (Boxgrove, Sidestrand and Westbury-sub-Mendip) and age group 4 (Untermassfeld) was significant ($\chi^2=34.058$, $N=242$, $p=0.0001$), indicating differences in the distribution of tooth wear, and that an association exists between tooth wear and age groups.

5.3.9.5. Tooth wear analysis: *C. etruscus* from Europe

All worn teeth were counted and tabulated (Table 5.179) for *C. etruscus* from Olivola and the Upper Valdarno. At both sites *C. etruscus* has a higher percentage of moderately worn teeth.

Faunal unit	Site code	Age group	Total n teeth	n and % teeth with wear category						n broken teeth
				Slight	%	Moderate	%	Heavy	%	
U. Valdarno	**UV**	4.4	73	29	39.7	29	39.7	15	20.6	4
Olivola	**OLV**	4.4	39	10	25.6	22	56.4	7	18.0	5
Tot. C. etruscus		*4.4*	*112*	*39*	*34.8*	*51*	*45.5*	*22*	*19.6*	*5*

Table 5.179. Tooth wear and breakage data for *C. etruscus* from Italy. Total number of teeth shown. Number of teeth assigned to wear category shown as counts and percentages. Rows in italics indicate the total number of teeth for each age group assigned to wear category also shown as total counts and percentages. Number of teeth identified as broken shown.

Site	Site code	Age group	Total n teeth	n and % teeth with wear category						n broken teeth
				Slight	%	Moderate	%	Heavy	%	
U. Valdarno	**UV**	4.4	81	45	55.6	29	35.8	7	8.6	1
Tot. C. arnensis		*4.4*	*81*	*45*	*55.6*	*29*	*35.8*	*7*	*8.6*	*1*

Table 5.180. Tooth wear and breakage data for *C. arnensis* from Italy. Total number of teeth shown. Number of teeth assigned to wear category shown as counts and percentages. Rows in italics indicate the total number of teeth for each age group assigned to wear category also shown as total counts and percentages. Number of teeth identified as broken shown.

Figure 5.111 illustrates the percentage of teeth with wear for the different sites.

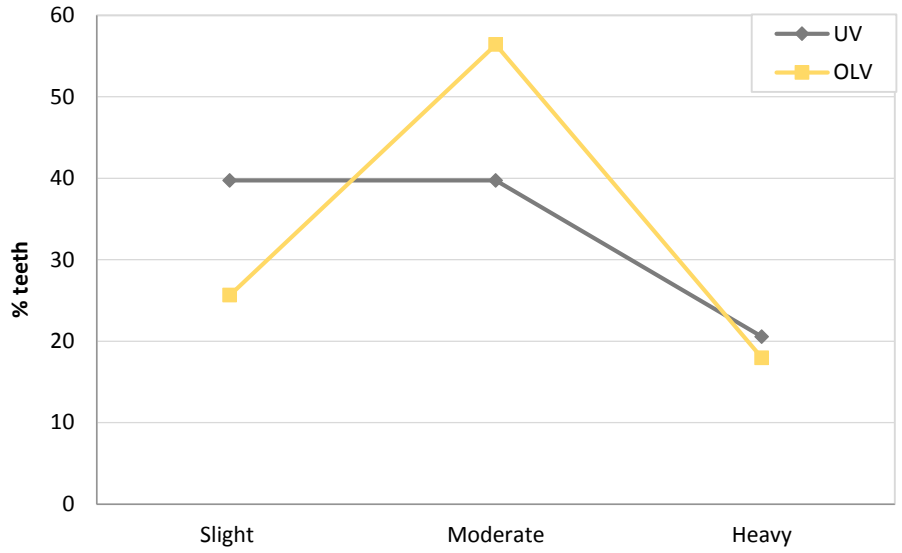


Figure 5.111. Percentages of worn teeth for *C. etruscus* by wear category from Olivola and the Upper Valdarno. Site codes listed in Table 5.179.

C. etruscus from both Olivola and the Upper Valdarno have similar distributions of tooth wear, with high percentages of moderately worn teeth and low percentages of heavy wear.

5.3.9.5.1. Statistical analysis of tooth wear

Tables 5.181a, b. show the results of two-way classification Chi square tests (using 2x2 contingency tables) for tooth wear in *C. etruscus* between Olivola and the Upper Valdarno.

			Wear			
			Slight	Moderate	Heavy	Total
Age	Upper Valdarno	Count	29	29	15	73
		Expected Count	25.4	33.2	14.3	73.0
	Olivola	Count	10	22	7	39
		Expected Count	13.6	17.8	7.7	39.0
Total		Count	39	51	22	112
		Expected Count	39.0	51.0	22.0	112.0

Table 5.181a. Cross-tabulation of counts and expected counts of numbers of teeth in tooth wear categories (slight (1), moderate (2), heavy (3)) for Olivola and the Upper Valdarno containing *C. etruscus*. Numbers illustrated used in Chi-square analysis in Table 5.181b.

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	3.090[a]	2	.213
Likelihood Ratio	3.117	2	.210
Linear-by-Linear Association	.637	1	.425
N of Valid Cases	112		

Table 5.181b. Results of Pearson Chi-square test for wear categories and Olivola and the Upper Valdarno for *C. etruscus*. a. 0 cells (.0%) have expected count less than 5. The minimum expected count is 7.66. Significance indicated by $p<0.05$.

The Pearson Chi-square for tooth wear in Olivola and the Upper Valdarno was non-significant (χ^2= 3.090, *N*=112, *p*=0.213), indicating no differences in the distribution of tooth wear, and hence no association was present between tooth wear and the sites containing *C. etruscus*.

5.3.9.6. Tooth wear analysis: *C. arnensis* from Europe

All worn teeth were counted and tabulated (Table 5.180) for *C. arnensis*. All data were from the Upper Valdarno, and thus comparisons of tooth wear were not possible. Figure 5.112 illustrates the percentage of teeth with wear for the Upper Valdarno.

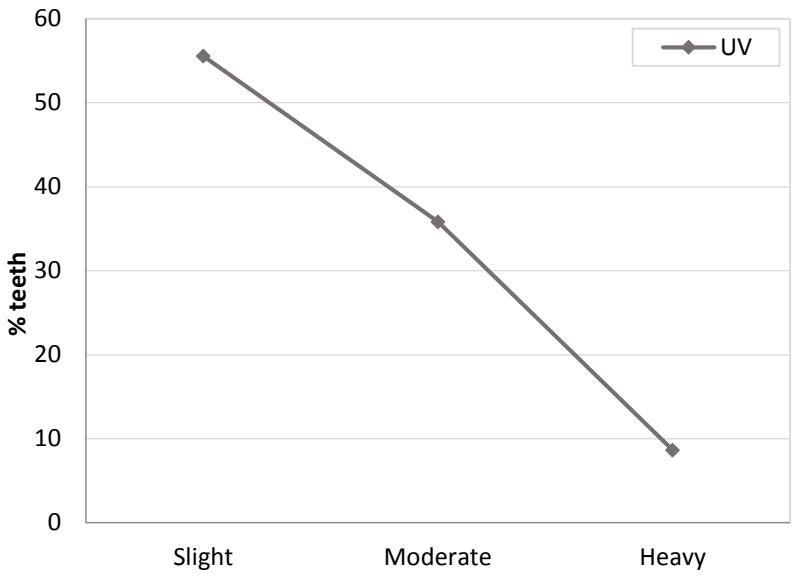


Figure 5.112. Percentages of worn teeth by wear category for *C. arnensis* in the Upper Valdarno. UV: Upper Valdarno.

C. arnensis has a high percentage of slightly worn teeth, combined with a low percentage of heavily worn teeth. Further analysis was not possible due to lack of comparative sites containing *C. arnensis*.

Summary

The frequency distribution of tooth wear was significant in *C. lupus* between MIS 3, 5a and 7, indicating that tooth wear in these age groups was related to factors other than ontogenetic age related wear. The presence of significant wear distributions correlates well

with the temporal differences found between these age groups and the dietary measurements.

It is interesting that for *C. lupus* from Europe in age groups 2.4 and 2.8 (mid and early Late Pleistocene) tooth wear distribution was non-significant. These age groups approximate to MIS 3 and all the MIS 5e-a in Britain, yet do not reflect the significant differences found in Britain at this time.

For *C. mosbachensis* from Britain, tooth wear distribution was non-significant between sites of MIS 13, correlating with the lack of temporal difference in the dietary measurements. However, when analysed with *C. mosbachensis* from Untermassfeld (age group 4, late Early Pleistocene), the distribution of tooth wear was significant, which was in contrast to the lack of temporal differences found in diet between these age groups.

The distribution of tooth wear in *C. etruscus* between Olivola and the Upper Valdarno was non-significant, which correlates well with the lack of temporal differences found in the cranio-dental measurements. Further analysis of *C. arnensis* was not possible due to lack of comparative material.

5.3.9.7: Tooth wear analysis: climate groups of *C. lupus* from Britain

The presence of tooth wear was assessed for the British climatic groupings of *C. lupus*, based on group 1 including MIS 3, 5a and 6 representing cold climatic conditions, and group 2 including MIS 5e and 7 are representing warm climatic conditions. Only British material was analysed due to the better constrained chronology of sites.

All worn teeth were counted and tabulated (Table 5.182) for *C. lupus* from Britain organised into the climatic groups.

Site	Site code	Age (MIS)	Tot. n teeth	n teeth & % with wear score						Tot. n broken
				Slight	%	Moderate	%	Heavy	%	
Black Rock Quarry	BRQ	3	23	5	21.7	7	30.4	11	47.8	0
Kents Cavern (Cave Earth)	KC	3	24	4	16.7	10	41.7	10	41.7	1
Oreston Cave	OSTN	3	44	14	31.8	22	50.0	8	18.2	2
Paviland	PAV	3	32	5	15.6	18	56.3	9	28.1	1
Pin Hole Cave	PHC	3	32	3	9.4	18	56.3	11	34.4	0
Sandford Hill	SFH	3	4	0	0	4	100.0	0	0	0
Uphill Cave	UPH	3	2	1	50.0	1	50.0	0	0	0
Banwell Bone Cave	BWL	5a	125	11	8.8	47	37.6	67	53.6	12
Bosco's Den	BSD	5a	23	6	26.1	9	39.1	8	34.8	2
Steetley Quarry	STQ	5a	4	0	0	2	50.0	2	50.0	0
Stump Cross Cave	SCC	5a	8	8	100.0	0	0	0	0	0
Windy Knoll	WK	5a	19	5	26.3	8	42.1	6	31.6	1
Wretton	WTN	5a	8	0	0	0	0	8	100.0	0
Clevedon Cave	CVD	6	39	3	7.7	18	46.2	18	46.2	3
Tot. cold grp 1			*387*	*65*	*16.8*	*164*	*42.4*	*158*	*40.8*	*22*
Barrington	BTN	5e	2	0	0	2	100.0	0	0	1
Joint Mitnor Cave	JMC	5e	47	25	53.2	17	36.2	5	10.6	1
Crayford	CYD	7	7	1	14.3	5	71.4	1	14.3	1
Hutton Cave	HTN	7	28	10	35.7	17	60.7	1	3.6	1
Ilford	ILF	7	5	4	80.0	1	20.0	0	0.0	0
Marsworth	MRSW	7	9	7	77.8	1	11.1	1	11.1	0
Pontnewydd Cave (L. Breccia & Int. Layer)	PNC	7	24	10	41.7	8	33.3	6	25.0	0
Tornewton Cave Otter Stratum	TNC OS	7	3	3	100.0	0	0	0	0	0
Tot. warm grp 2			*125*	*60*	*48.0*	*51*	*40.8*	*14*	*11.2*	*4*

Table 5.182. Tooth wear and breakage data for climate groups of *C. lupus* from Britain. Total number of teeth shown. Number of teeth assigned to wear category shown as counts and percentages. Rows in italics indicate the total number of teeth for climate groups 1 (MIS 3, 5a, 6) and 2 (MIS 5e, 7). Number of teeth identified as broken shown.

Figure 5.113 summarises the percentage of teeth with categorised tooth wear in the cold and warm climate groups.

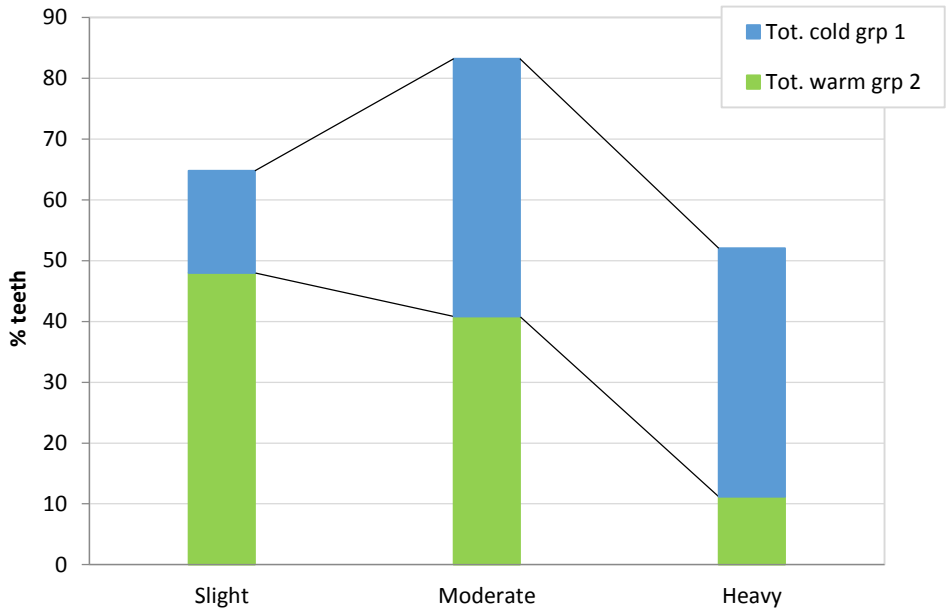


Figure 5.113. Summary of the percentages of worn teeth by wear category in climate groups of *C. lupus* from Britain. Cold group 1: MIS 3, 5a, 6, and warm group 2: MIS 5e and 7.

The cold climate group (1) has the highest percentage of heavily worn teeth, with similar proportions of moderately worn teeth and much lower numbers of slightly worn teeth. In contrast, the warm climate group (2) has the highest percentage of slightly worn teeth, with similarly high number of moderately worn teeth, and correspondingly low numbers of heavily worn teeth.

5.3.9.7.1. Statistical analysis of tooth wear

Table 5.183a, b shows the results of two-way classification Chi-square tests (2x3 contingency table) for tooth wear between cold and warm climatic groupings.

			Wear			
			Slight	**Moderate**	**Heavy**	**Total**
Climate group	Cold group	Count	65	164	158	387
		Expected Count	94.5	162.5	130.0	387.0
	Warm group	Count	60	51	14	125
		Expected Count	30.5	52.5	42.0	125.0
Total		Count	125	215	172	512
		Expected Count	125.0	215.0	172.0	512.0

Table 5.183a. Cross-tabulation of counts and expected counts of numbers of teeth in tooth wear categories (slight (1), moderate (2), heavy (3)) for climate groups 1 (MIS 3, 5a, 6) and

group 2 (MIS 5e, 7) containing *C. lupus* from Britain. Numbers illustrated used in Chi-square analysis in Table 5.183b.

	Value	df	Asymp. Sig. (2-sided)
Pearson Chi-Square	62.425[a]	2	.0001
Likelihood Ratio	63.422	2	.0001
Linear-by-Linear Association	61.041	1	.0001
N of Valid Cases	512		

Table 5.183b. Results of two-way Chi-square test for wear categories and climate groups 1 (MIS 3, 5a, 6) and group 2 (MIS 5e, 7) for British *C. lupus*. a. 0 cells (.0%) have expected count less than 5. The minimum expected count is 30.52. Significance indicated by $p<0.05$.

The Pearson Chi-square for tooth wear scores in the warm and cold climate groups was significant ($\chi^2=62.425$, $N=512$, $p=0.0001$), indicating differences in the distribution of tooth wear, and an association between tooth wear and the climate groups existed.

Summary

In similarity to the differences found in the frequency distributions of tooth wear in MIS 3, 5a and 7, the frequency of tooth wear in the cold and warm climate groupings were also significant, indicating factors other than ontogenetic age were responsible for the variation in tooth wear.

Canid evolution and palaeoecology in the Pleistocene of western Europe, with particular reference to the wolf *Canis lupus* L. 1758.

Volume 2

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6. Discussion

The following chapter will discuss the results from the estimation of body size and analysis of palaeodiet, in relation to temporal, climatic and environmental variation, carnivore community structure and competition.

6.1. Canid body mass from the Early, Middle and Late Pleistocene

As introduced in Chapter 3, body mass (a surrogate for body size), is one of the most important ecological factors affecting canids, dictating ecological niche via prey choice, as well as influencing hunting strategy and hunting behaviour. Changes in body mass can cause major changes in community structure and resource partitioning, leading to increased competition and potential dietary adaptation. Understanding the causes of body mass change (and particularly the interplay of climate, environment and community factors) is therefore of great importance in carnivore evolution.

The body masses of the Pleistocene canids were therefore investigated in order to elucidate the palaeoecology of each species, allowing inferences regarding prey choice and community dynamics to be made and the potential effect of climate change (through Bergmannian responses) to be evaluated. The presence of any temporal differences in body mass was also examined, in order to determine whether palaeoecology of individual species changed over time and why this occurred.

6.1.1. Validation of the regression model and predictive problems

The least squares regression of extant canid body mass and carnassial length created a predictive equation for the estimation of Pleistocene canid body mass. However, examination of the regression analysis indicated the presence of outliers in the model that were highly influential and had high leverage, and required removal to validate the predictive model.

In the regression using m1L, three species were excluded: raccoon dog (*Nyctereutes procyonoides*), bat-eared fox (*Otocyon megalotis*) and Rüppell's fox (*Vulpes rueppellii*). The first two are both less derived members of uncertain position within the basal Caninae and, in the case of *O. megalotis*, possess highly unusual dental morphology in comparison to other canids (Guilday, 1962; Keiser, 1995). *V. rueppellii*, on the other hand, is securely a member of the genus *Vulpes* but may be an outlier on account of its small size. The removal

of these species left the regression model free from detrimental outliers and suitable for predictive use. Regressions using m1L and P4L were compared and the former was chosen as providing the better predictive model for body mass estimation, with higher r^2 (r^2=0.937), and lower %SEE (25.75%) and %PE (17.41%) than P4L.

As introduced in Chapter 4, the r^2, %SEE and %PE are used comparatively to gauge predictive precision and power of the regression equation. The correlation between m1L and body mass was indeed very high, indicating a strong predictive relationship. The lower %SEE for m1L than for P4L found the equation to have a higher level of precision, combined with a relatively low %PE, also indicating higher predictive accuracy of the equation.

Nonetheless, although the %SEE and %PE are considered low here, lack of predictive precision is commonplace in body mass estimations. To minimise precision errors, a large dataset of extant canids was used to try to reduce the effect of phylogeny. The presence of outliers in the regression residual data was also checked, to ensure the strongest predictive equation possible was created. However, a potential source of error may lie in the use of combined male and female means of extant body mass and carnassial measurements in the model, meaning variation between the sexes was not accounted for. Nevertheless, canid sexual dimorphism is generally low and thus the use of combined means was not considered problematic. The use of mean data was also considered to reduce potential errors by eliminating individual variability (Ruff, 2003).

Ultimately, the most likely source of precision error may relate to the choice of m1L. Van Valkenburgh (1990) stated that head-body length (%SEE 24, %PE 17), skull length (%SEE 31, %PE 21) and occiput-orbit length (%SEE 30, %PE 22) were all better predictors of body mass in canids than m1 length (%SEE 44, %PE 27), yet the predictive m1L equation used here actually has higher precision (%SEE 25.75, %PE 17.41). In Van Valkenburgh's (1990) study, head-body length is most similar in terms of predictive precision to that of the m1L equation used here. Similarly, in Anyonge's (1993) study using canid post-cranial characters, femoral circumference was found to be the best predictor of body mass, based on %SEE 23, %PE 18. Again, the level of precision using femoral circumference is similar to the precision of m1L used here. Head-body length is very rarely preserved in the palaeontological record and both post-cranial and cranial material are often fragmentary. In contrast, teeth are often abundant and well-preserved, leading to the wide use of m1L in body mass estimation, and justification of the approach taken here.

From the examination of scaling between carnassial length and extant canid body mass, the allometric coefficients (*b*) were both greater than the expected allometric coefficient representing isometry (*b* =0.333) for both m1L (*b* =0.379) and P4L (*b* =0.376), thus indicating both to be positively allometric with respect to body mass. However, statistically testing for significant differences between these coefficients and isometry revealed that m1L was significantly different from isometry, whilst P4L was found to be similar, and thus not significantly different from isometry.

These differences were surprising, and may relate to differences in standard error of slope and degrees of freedom between the two regression models. Nonetheless, m1L was indicated as positively allometric, and thus with any increase in body mass, m1 length increases at a faster rate. It is therefore possible that m1 length is slightly overestimating predicted body size. Even though m1 length may represent a slight overestimation of body mass, it still had higher predictive precision than P4L. Thus, the potential for overestimation of body size is a caveat in the body mass analysis.

This highlights the need for other predictors of body mass to be included in the analyses, although this is hampered by incomplete material. m1L and P4L were more abundant in comparison to other potential predictors, in particular complete lower carnassials. Thus, although the use of m1L may have some problems, its use is fully justified and the predictive model created compares favourably with other published predictive equations.

6.1.2. Temporal differences in body size: palaeoclimatic and palaeoenvironmental implications

The presence of temporal differences in estimated body size for the Pleistocene canids will be discussed in the following sections, together with the impacts of changing palaeoclimate, palaeoenvironment and palaeogeography.

6.1.2.1. Body mass estimations of *Canis etruscus* and *Canis arnensis*

Body mass of *C. etruscus* was estimated using m1L from individuals present at Val di Magra (Olivola F.U.) and sites of the Upper Valdarno basin (Tasso F.U.). Combined, the mean estimated body mass for *C. etruscus* was 24.34 ± 1.65Kg, with a mass of 25.55 ±2.70Kg estimated for Olivola, and lighter (although overlapping in confidence intervals) at 23.91 ± 1.69Kg for the Upper Valdarno. This slight difference in mean mass is interesting, indicating

that *C. etruscus* reduced in size over a relatively short period of time. Both body mass estimates for *C. etruscus* are above Carbone et al.'s (1999) dietary threshold limit of 21.5Kg, implying an ability to hunt prey of similar or larger size than itself (see 6.3 later).

Other estimates of body mass were made by Garcia and Virgos (2007) for *C. etruscus* from the Upper Valdarno using m1L, which predicted mass of 16.82 Kg. This is a much lighter estimate than the one generated here and little information is given as to the precision of the equation. However, the lighter prediction may relate to the broader range of carnivores used by these authors to model body mass. This is in contrast to the equation created here, which was canid family based, and included a higher number of species. Similarly, the body mass equation created by Van Valkenburgh (1990) for canids predicted slightly lower body mass at 21.23 ±4.85Kg but the higher %SEE and %PE render this a less precise estimate.

In terms of comparability with living canids, the mean *C. etruscus* estimate was most similar to *L. pictus* (mean 24.83Kg, range 20-32Kg [Macdonald, 2009]) and *Chrysocyon brachyurus* (mean 23Kg [Dietz, 1985; Macdonald, 2009], no range given). The estimated body mass also is within the lower part of the range of modern *C. lupus* (mean 41.33Kg, range 18-80Kg [Mech, 1974]), although modern wolves have a much larger range. Thus, with body size being correlated with prey size, inferences on the prey choices of *C. etruscus* can be made. Additional dietary comparisons and discussion of palaeoecology are made in section 6.3.

Body mass of *C. arnensis* was also estimated from the Upper Valdarno (Tasso F.U.) only, and thus no temporal comparisons were possible. Mean body mass was estimated as 17.94 ±1.73Kg for *C. arnensis*, revealing it to be of smaller size than sympatric *C. etruscus* at this time. In contrast to *C. etruscus*, this estimate is below the dietary threshold limit of 21.5Kg, indicating that *C. arnensis* was not able to hunt prey larger than itself, and was therefore a predator of small prey. The ramifications of this in relation to the other Upper Valdarno canids will be further discussed in relation to diet in section 6.3.

Body mass of *C. arnensis* from the Upper Valdarno was estimated using m1L as 13.2Kg by Garcia and Virgos (2007). As with the predicted mass for *C. etruscus* by the same authors, this estimate is also much lighter than the one generated by this research. As discussed above, the reasons for this may lie in the broader carnivore dataset used by the authors, rather than the large canid family dataset used here.

Van Valkenburgh's (1990) predictive equation estimated body mass at 16.90 ±2.40Kg, again slightly lighter than the outcome of this research, yet within its confidence interval range.

Although the Van Valkenburgh (1990) equation has lower predictive ability, it is nonetheless useful for comparing predicted body masses since it is based on the same dental characteristic.

The estimated body mass of *C. arnensis* was also compared to the masses of extant canids, in order for inferences regarding palaeoecology to be made. *C. arnensis* was found most similar to *C. alpinus* (mean 16.93Kg, with a range of 10-20Kg [Cohen, 1978]), although towards the large end of size range. *C. arnensis* also was in range of both *C. simensis* (mean 15.6Kg, with a range of 11.2-19.3Kg [Sillero-Zubiri and Gottelli, 1994]) and *C. latrans* (mean 14.25Kg, with a range of 7-20Kg [Bekoff, 1977]).

Further comparisons with extant canids will be made in relation to palaeodiet in 6.2 and 6.3. Of particular interest is the size similarity with *C. latrans*, since *C. arnensis* is often compared to the coyote on cranio-dental characters (Martinez-Navarro and Rook, 2003; Sardella and Palombo, 2007). However, *C. arnensis* has also been likened to jackals (Torre, 1967; Kurtén 1968), which interestingly do not overlap with *C. arnensis* in terms of their mean body mass or size ranges: *C. adustus* (mean 10.8Kg, range 6.5-14Kg [Macdonald, 2009]), *C. mesomelas* (mean 8.75Kg, range 5.9-9.9Kg (Loveridge and Nel, 2004), *C. aureus* (mean 11Kg, range 6.5-14Kg [Macdonald, 2009]).

As body mass is linked to prey size and therefore diet, the observed body mass differences with jackals and similarities to coyotes is notable, potentially supporting the opinions based on morphology (e.g. Kurtén, 1974) that *C. arnensis* was more like coyotes than jackals in terms of its palaeoecology. However, as *C. arnensis* was also of similar size to *C. alpinus*, the diet of *C. arnensis* needs to be considered before ecological correlates can be fully identified.

6.1.2.1.1. Palaeoclimatic and palaeoenvironmental interpretation

For *C. etruscus*, although both Olivola and the Upper Valdarno specimens have been separated for temporal analysis here, both sites are relatively close in age in the middle Early Pleistocene (late Villafranchian, approximately ~1.9 and ~1.8Ma respectively). The assemblages from Olivola and Upper Valdarno are conventionally separated into discrete faunal units (Olivola F.U. and Tasso F.U.), although this was challenged by Raia et al. (2006) who considered that although the sites were of different age, the two faunal units should be combined as one local palaeocommunity.

From the canid perspective, the expansion of the canid guild in the Upper Valdarno represented a fundamental change for *C. etruscus*, from being a lone canid at Olivola, to being part of a perhaps more competitive cursorial group. The difference in mean body mass in *C. etruscus* between Olivola and the Upper Valdarno was perhaps a response to the arrival of these additional canids, which has been linked to the spread of increasingly open grassland environments favourable for cursorial species (Petronio *et al.*, 2011).

Prior to *c.* 1.2 million years, the Early Pleistocene was dominated by 41 ka obliquity cycles (Shackleton *et al.*, 1990), causing increased seasonality but with only modest variations in palaeotemperature and no major glaciations in the northern hemisphere. Starting around 1.2 Ma, a switch to eccentricity-dominated orbital periodicity resulted in much more intense glacial-interglacial cycles occurring every 100 ka. The cause of these changes is still matter of debate (cf. Maslin *et al.,* 2001) but the switch is termed the "Mid-Pleistocene Revolution", also known as the "Mid-Pleistocene Transition". This point marks a pronounced intensification in these glacial-interglacial cycles and is the last major event in a secular trend towards more intensive global glaciation.

In Italy, where the earliest evidence for the wolf lineage is present, the climate of this period was characterised by relatively rapid alternations between moist and arid conditions, with fluctuations between warm-temperate deciduous woodland and steppe with coniferous forest (Masini and Sala, 2007; Bertini *et al.*, 2010). During cooler phases, the peninsula was divided into two climatic zones, the north characterised by moister conditions and presence of coniferous forests, and the south being drier with steppic vegetation (Bertini, 2003).

Both Olivola and the Upper Valdarno were characterised by the general trend of cooling climatic conditions of the Late Villafranchian (Bertini, 2003), as well as the gradual loss of forest and progression towards open grassland environments. Both sites are located centrally in the peninsula, where drier conditions would have been more influential, and during these cool, arid phases, hardy herbaceous plants such as *Artemisia* and shrubs of *Ephedra* would have been in abundance (Kahlke *et al.*, 2011).

The expansion of steppic environments led to the progressive dispersal of open landscape taxa, whereas woodland taxa declined (Bertini *et al.*, 2010). Both the Olivola F.U. and Upper Valdarno Basin (Tasso F.U.) were characterised by a highly diverse range of ungulates, typically including open environment indicator species.

Olivola was characterised by numerous grazing and browsing ungulates, indicative of a mosaic of open grassland and wooded environments, such as the deer *Eucaldoceros dicranios-ctenoides* and *Pseudodama nestii,* and the chamois-like *Procamptoceras brivatense*, as well as large herd animals including the bovid *Leptobos etruscus* and the zebrine horse *Equus stenonis* (Gliozzi *et al.*, 1997; Kahlke *et al.,* 2011, see Appendix 1.35 for the full species list). The carnivores similarly reflect mixed conditions, with *C. etruscus* and the short-faced hyaena *Pachycrocuta brevirostris* favouring open grassland and the jaguar-like *Panthera gombaszoegensis* occupying more wooded environments. The interactions between carnivores and prey will be further discussed in section 6.3.

The transition between Olivola and Tasso F.U.s was marked by a peak in aridity and relatively cooler conditions (Caloi and Palombo, 1997), and was marked by gradual turnover in faunal composition (Masini and Sala, 2007) and an increase in species diversity (Kahlke *et al.*, 2011).

The Early Pleistocene in Italy was characterised by a gradual lowering of mean temperature, inducing a change from forest to increasingly open grassland environments (Petronio *et al.*, 2011). A mean annual temperature of 17.36°C was estimated for the Tasso F.U. (Montuire and Marcolini, 2002), which is indicative of similar to slightly warmer climatic conditions than are present in this region of Italy today. Based on progressive lowering of temperatures, it is possible that Olivola was slightly warmer than the Upper Valdarno.

A recent palaeobotanical study by Bertini (2013) identified a cool dry phase at the start of the Tasso F.U. in the Upper Valdarno basin, which correlates well with the continued expansion of open environments, and the appearance of additional cursorial canids and a wider range of grazing herbivores in the fossil record. Sporadic occurrences were also noted of flood-tolerant conifers *Taxodium* and *Glyptostrobus*, which are associated with ephemeral freshwater wetlands (Bertini, 2013). Like Olivola, the assemblages of the Upper Valdarno Basin were also characterised by a combination grazers, mixed feeders and browsers, many of which survived the Olivola-Tasso F.U. transition such as *L. etruscus* and *E. stenonis*, and including new arrivals such as an ovibovine *Praeovibos* sp, deer *Pseudodama eurygonas-farnetensis*, small horse *Equus stehlini* and bovid *Leptobos vallisarni* (Rook and Martinez-Navarro, 2010) (see Appendix 1.36 for the full faunal list). *C. falconeri* and *C. arnensis* both appeared during the Tasso F.U. and their interactions within the carnivore community will be further discussed in section 6.3.

Overall, both Olivola and the Upper Valdarno were characterised by similarly open grassland conditions and an overall temperate climate. Palaeoclimatic oscillations, although present, were comparatively muted. It is therefore possible that the decrease in body mass found between Olivola and Upper Valdarno *C. etruscus* was related to changes in the carnivore community, in particular to the increase in canid guild members, which will be further discussed in section 6.3. Unfortunately, because of the limited material available, it was not possible to determine whether *C. arnensis* experienced body mass change through time.

6.1.2.2. Body mass estimation of *Canis mosbachensis*

The overall mean body mass of *C. mosbachensis* was estimated as 22.50 ± 1.62Kg, with Britain estimated as 22.47 ± 1.69Kg, and mainland Europe as 22.22 ± 1.67Kg. In terms of these regional estimates, *C. mosbachensis* was just over the dietary threshold weight of 21.5Kg, indicating that it could hunt prey of a similar size or larger than itself (see 6.3).

Body mass estimations were made for *C. mosbachensis* from Venta Micena in Spain by Palmqvist et al. (1999, 2002, 2008), using multiple regression of upper canine length and mandible length, indicated a mass of 10.8Kg, with a range of 5.4-21.6Kg, whereas upper canine length and P4 width estimated 6.2Kg, with a 3.3-11.7Kg range. Both estimates are substantially lighter than the ones created here. Although these authors built their predictive model also using a large canid based dataset, the overrepresentation of one predictor over another was considered a potential cause of underestimation for the latter equation in particular (Palmqvist *et al*., 2002). The Van Valkenburgh (1990) equation estimated *C. mosbachensis* body mass as 20.03 ±2.16Kg, also giving a slightly lighter estimate than the one proposed here.

In comparison to the earlier Pleistocene canids, *C. mosbachensis* was closer in size to *C. etruscus* (24.34 ± 1.65Kg) and larger than *C. arnensis* (17.94 ±1.73Kg). As discussed in Chapter 2, rather than being part of the wolf lineage, *C. mosbachensis* has been associated with *C. arnensis* (Garrido and Arribas 2008; Martinez Navarro *et al.*, 2009) and considered more similar to modern jackals based on size and dentition (Martinez Navarro *et al.*, 2009).

It is therefore interesting that from the body mass estimates here, *C. mosbachensis* has a closer size affinity with *C. etruscus*, and hence based on the relationship between body size and prey size, as well as its influence of ecology, it seems that *C. etruscus* and *C. mosbachensis* were perhaps closer palaeoecologically. The differences in size estimates

between *C. mosbachensis* and *C. arnensis* place them on either side of the dietary threshold weight (21.5Kg), indicating differentiation in prey targeting ability. These differences in size, combined with the dietary analysis will be discussed further in section 6.3.

In comparison to extant canids, *C. mosbachensis* was most similar in body mass to *Chrysocyon brachyurus* (mean 23Kg, no published range), as well as *L. pictus* (mean 24.83Kg, range 20-32Kg [Macdonald, 2009]), although with *C. mosbachensis* towards the lower end of that size range. Thus, inferences on potential prey sizes may be possible through analogy although, as indicated previously, both maned wolf and hunting dog have specific dietary adaptations that will be discussed further in 6.3 with respect to *C. mosbachensis*.

C. mosbachensis is often compared to jackals, although the body mass estimates here show it to be larger than *C. adustus* (mean 10.8Kg, range 6.5-14Kg [Macdonald, 2009]), *C. mesomelas* (mean 8.75Kg, range 5.9-9.9Kg [Loveridge and Nel, 2004]), and *C. aureus* (mean 11Kg, range 6.5-14Kg [Macdonald, 2009]), indicating that size comparisons with jackals may be inappropriate. The palaeodietary implications and differences in diet between *C. mosbachensis* and the jackals will be discussed in section 6.2.

6.1.2.2.1. Palaeoclimatic and palaeoenvironmental interpretation

The similarity between the estimates for *C. mosbachensis* is striking considering that the samples examined here span a large time range of 660,000 years, from the late Early Pleistocene to the Middle Pleistocene. The comparability is also marked in view of the palaeogeographical distance between the British, German and Italian material. The results will be discussed below in the context of regional differences in palaeoclimate and palaeoenvironment, based on age group as well as by site where applicable.

6.1.2.2.1.1. Pleistocene mainland Europe

As introduced in Chapter 4, broad age groups were constructed for the less well-dated mainland Europe sites in order to increase the amount of comparable material for analysis. Nonetheless, body mass was only estimated for age group 4 (late Early Pleistocene) and 3.4 (mid Middle Pleistocene) due to low numbers of individuals in the other groups. No British Early Pleistocene material was available, due to a paucity of sites, and thus comparisons

with individuals of a similar age on the continent were not possible. These continental sites nevertheless provide valuable evidence for extending the age range of *C. mosbachensis*, which is only recorded in early Middle Pleistocene in Britain, allowing a fuller overview of the temporal range of this species.

For age group 4 (late Early Pleistocene), the only site containing high enough numbers of m1 for use in body mass estimation was Untermassfeld, which has been dated to just older than 1 Ma (Kahlke *et al.*, 2011). Here, mean body mass for *C. mosbachensis* was estimated as 23.14 ± 1.71Kg. The site of Untermassfeld has been reconstructed as a valley flood plain with a dynamic river system (Kahlke, 2000), encompassing a mixed environment with higher and drier areas away further from the river and lower, more flood-prone areas next to the river. In the higher areas, mixed forest and herbaceous vegetation persisted, whereas the flood-prone areas supported low growing forest, as well as meadows, swamps and ponds (Kahlke 2000).

This varied landscape conditions supported a diverse range of species, with the presence of cursorial canids such as *C. mosbachensis* and *C.* (*X.*) *lycaonoides*, grazers such as bison *Bison menneri* and *Mammuthus* sp. indicative of open landscapes, aquatic species such as hippopotamus *Hippopotamus amphibius antiquus* and giant beaver *Trogontherium cuvieri*, and closed woodland species such as the lynx *Lynx issiodorensis* and macaque monkey *Macaca sylvanus* (see Appendix 1.37 for the full species list). The presence at Untermassfeld of thermophilous taxa such as European pond tortoise (*Emys orbicularis*) and hippopotamus are indicative of warmer than present interglacial conditions. The reproductive success of pond tortoise relies on specific and consistent ecological conditions, such as hours of sunlight, as well as mean July temperatures of 17-18°C (Stuart, 1979), whereas mean winter temperatures above freezing are required for the aquatic habitats of hippopotamus, as well as warmer than present summer temperatures (Stuart, 1976).

As stated, no regional comparisons were possible for Untermassfeld, however, comparisons with younger sites from early Middle Pleistocene Britain, as well as with the Middle Pleistocene of both Britain and Europe were possible. For mainland Europe, age group 3.4 (mid Middle Pleistocene) represents a spread of sites covering the broad time period MIS 12-9. The estimated mean body mass for this age group was 20.52 ± 18.50Kg, based on individuals from Heppenloch and Monte Zoppega. Although this estimate is lighter than at Untermassfeld, the large confidence intervals indicate the imprecision in the

range of this estimate. Heppenloch has been correlated with MIS 11 (Kahlke *et al*., 2011) although the age of Monte Zoppega is less secure, described only as the Mindel-Riss interglacial by Bon et al. (1991), which in the current understanding of late Middle Pleistocene climatic complexity could cover either or both MIS 11 and 9. The mean body mass estimate for age group 3.4 thus represents *C. mosbachensis* of MIS 11 and potentially MIS 9 age on the continent. Both sites are characterised by differing regional influences, namely the central European climate for Heppenloch and peninsula status for Monte Zoppega.

Following the Mid-Pleistocene Revolution around 1.2 Ma, northern Europe began to experience the first major land-based glaciations. By 800 ka, the 100ka eccentricity-dominated glacial-interglacial cycles were fully established (Ehlers and Gibbard, 2007), with the notably cold period of MIS 22 (approx. 0.87 Ma) the first major cold event that led to substantial continental ice volumes equivalent to later Pleistocene glaciations (e.g. MIS 16, 12, 6 and 4-2) (Ehlers and Gibbard, 2007). The cold period correlated with MIS 16 (~630 Ka, within the Cromerian Complex) was also particularly severe, with evidence of ice sheet formation in Eastern Europe from the Don Till (Ehlers and Gibbard, 2007). Evidence for glaciation during MIS 16 is also present in eastern Britain, which will be discussed in the next section.

The Elsterian glaciation, correlated with MIS 12 (~0.45 Ma), was long-lasting and intensely cold in central Europe, and represented the largest advance of the Baltic ice sheet into the region (Kahlke *et al.*, 2011). During this time, the first appearance of the *Mammuthus-Coelodonta* faunal complex occurred in central Europe, reflecting the spread of cold adapted fauna (Kalhke, 1999).

The prevailing conditions during the early Middle and Middle Pleistocene in central Europe were warm-humid to cool-dry, characterised by alternating woodland, steppe, and tundra during the coldest periods (Kahlke *et al.*, 2011). MIS 11 in particular was distinctive in central Europe by its extensive forests and warm humid climate (Kahlke *et al.*, 2011), although Heppenloch was characterised by relatively more open conditions due to the lack of woodland indicator species of giant deer and Merck's rhinoceros (Adam, 1975) (see Appendix 1.40 for full species list).

In the Apennine peninsula, the early Middle and Middle Pleistocene saw an increase in more steppic conditions (Kahlke *et al.*, 2011), and was also characterised by consistent faunal renewal between the Early Middle Pleistocene Slivia F.U. (MIS 22, 0.9 Ma) and

Isernia F.U. (0.7 Ma), with the final loss of all Villafranchian species by the Ranuccio F.U. (0.45 Ma) (Caloi and Palombo, 1997). Monte Zoppega contained both open landscape species such as *C. mosbachensis* and lion *P. leo*, as well as woodland species such as straight-tusked elephant *Palaeoloxodon antiquus* and fallow deer *Dama cf dama*, together wtih hippopotamus, indicating both warm conditions and a mixed environment.

The putative decrease in size of *C. mosbachensis* between the late Early and Middle Pleistocene is interesting and any potential trends will be discussed further with reference to the British early Middle Pleistocene. Unfortunately no comparison was possible with British sites equivalent to age group 3.4, since only one individual is present (from Grays Thurrock) with a measureable m1.

6.1.2.2.1.2. Pleistocene Britain

No body mass estimates for *C. mosbachensis* were possible from MIS 9 and 17, since the datasets for both were inadequate. For MIS 9, the only site representing this age group, Grays Thurrock, contains a lone individual, whereas sites of MIS 17 age did not contain any m1s for measuring. Hence, the earliest body mass estimates for *C. mosbachensis* in Britain are from MIS 13, where the mean estimated body mass was 22.07 ± 1.71Kg. This estimate contained individuals from Boxgrove, Sidestrand and Westbury-sub-Mendip, and is slightly lighter than (although within range of) the late Early Pleistocene sample from Untermassfeld (23.14 ± 1.71Kg).

However, in order to place the MIS 13 estimates in their climatic context, the prevailing climatic conditions in Britain during the early Middle Pleistocene need to be clarified. As discussed in the previous section, after 1.2 Ma northern Europe experienced the first major land-based glaciations. In Britain, the Anglian glaciation was considered to be the only major Middle Pleistocene glacial event in eastern Britain (Bowen *et al.*, 1986), with the glacial stratigraphy of East Anglia emplaced during a single cold stage during MIS 12 (Bowen, 1999). This was challenged by Hamblin et al. (2005), who proposed numerous Middle Pleistocene glaciations occurred correlated to MIS 16, 12, 10, as well as MIS 6.

In particular, the Happisburgh and Corton tills in eastern Britain were attributed to an older glaciation, correlated with MIS 16 (630 ka) and considered separate to the Anglian glaciation of MIS 12 (Hamblin *et al.*, 2005). Supporting evidence from sedimentology and river terrace stratigraphy for an earlier MIS 16 glaciation is reviewed in Rose (2009, and references therein). Based on the British evidence, combined with evidence from Europe

during MIS 16 as discussed, Rose (2009) considered that an extensive British ice sheet at this time was not an unreasonable conclusion.

Nevertheless, controversy remains with the proposed multiple Middle Pleistocene glaciations. From an extensive study of biological material from Sidestrand, which underlies the Happisburgh Till, Preece et al. (2009) provide palaeoenvironmental evidence from mammal, beetle and molluscan assemblages from Sidestrand that do not support the Happisburgh Till being of MIS 16 age. Of particular note is the presence of *Arvicola terrestris cantiana* beneath the Happisburgh Till, which first appeared during MIS 15 in continental Europe (Preece and Parfitt, 2000). Thus, the Happisburgh Till cannot be as old as MIS 16 and is more likely to represent an individual glacial advance within a complex Anglian glaciation (Preece *et al.* 2009), which remains the most far-reaching ice sheet in Britain.

The record of any cold-climate faunas prior to the Devensian in Britain is, however, extremely poor. The early Middle Pleistocene (Cromerian Complex) sites containing *C. mosbachensis* in Britain all represent temperate-climate conditions, although there is considerable variation between them. The Cromerian Complex is characterised by a succession of climatic episodes, with evidence for at least six distinct temperate phases (not all full interglacials) between ~780-450 ka (Preece, 2001). Although no body mass estimations were possible, the Cromerian type-site of West Runton, correlated with MIS 17 (Stuart and Lister, 2010), is characterised by fully interglacial conditions similar to Britain today, based on Coleoptera and Molluscan evidence.

Using the Mutual Climate Range (MCR) method (Atkinson *et al.*, 1987), Coope (2010) determined maximum peak summer temperature was 16-19°C, and minimum peak winter temperature was -3 to 5°C at West Runton, similar to the present day. Preece (2001, 2010) identified freshwater molluscs remarkably similar to the modern faunas present in eastern England but with the suggestion of more continental climatic conditions based on the presence of some species now inhabiting central and eastern Europe (e.g. *Bithynia troschelii*, *Marstoniopsis insubrica*).

The rich mammal faunal assemblage at West Runton (see Appendix 1.1 for the full list), is indicative of mixed landscape environment with wooded and open areas (Stuart and Lister, 2010), with temperate woodland species such as *M*. *sylvanus* present, as well as open indicator species such as steppe mammoth *Mammuthus trogontherii* and equids *Equus* cf. *sussenbornensis* and *Equus* cf. *altindens*. Carnivores occupying both grassland and more

closed woodland environments include *P. gombaszoegensis, Homotherium latidens, P. leo*, as well as *C. crocuta*. The palaeodietary implications of this carnivore guild are discussed in 6.3.

Both Westbury and Boxgrove, at the younger end of the early Middle Pleistocene, were also characterised by temperate conditions, although there is evidence of palaeoclimatic complexity at both localities. At Westbury, which appears marginally older than Boxgrove on the basis of its micromammalian fauna (Preece and Parfitt, 2000), the assemblages suggest the presence of at least two temperate climatic episodes separated by cooler conditions, within a single complex interglacial period (Schreve *et al.,* 1999). The first temperate episode contains very rich and diverse fauna, containing both open grassland species such as *Bison* cf *priscus* and *Equus caballus*, and woodland species of *Dama* sp. and *P. gombaszoegensis* (see Appendix 2.1 for the full species list). The units representing cooler conditions contain a paucity of species, whilst the second temperate episode, although less diverse, contains remains of numerous carnivores reflecting their increased use of caves. Both *C. mosbachensis* and *C.* (*X.*) *lycaonoides* are present throughout, with numerous other carnivores present such as *C. crocuta* and *H. latidens*, which will be discussed in section 6.3.

In comparison, the younger faunal assemblage at Boxgrove shows gradual increase in open environments, plus progressively cooler conditions. In the lower units of the assemblage, mixed woodland indicators such as *Apodemus sylvaticus* and *Dama dama* are present, whilst over time, cooler climatic indicator species such as *Microtus gregalis, Clethrionomys rufocanus* and *Lemmus lemmus* become more common (Parfitt, 1999) (see Appendix 1.3 for the full species list).

Similar in age to Boxgrove, the fauna from Sidestrand is indicative of mixed woodland, from presence of *A. sylvaticus* and *Felis sylvestris*, as well as open grassland from *Bison priscus* and *Equus süssenbornensis* (see Appendix 1.4 for the full species list). Preece et al. (2009) reconstructed mean summer temperatures of 16-24°C and mean winter temperatures of -9 to 9°C, highlighting that Sidestrand contained evidence for a thermal maximum in excess of both the present day and West Runton.

The early Middle Pleistocene in Britain was therefore climatically complex, with evidence for multiple temperate episodes that were warmer than, the same as, or cooler than southern Britain today (Candy *et al*., 2010). It is also important to note that during the Early and early Middle Pleistocene, a terrestrial connection existed between Britain and

mainland Europe, enabling free movement and faunal exchange between regions and thus (to a certain degree) homogenising faunal assemblages.

Estimates of body mass were made for Westbury and Boxgrove, with *C. mosbachensis* at Westbury estimated as 22.35 ±1.90Kg, comparable in size to Untermassfeld. For the younger Boxgrove, however, body mass was estimated as 20.34 ±18.50Kg, with the large confidence intervals due to the low number of individuals present (n=3). No estimates were possible for Sidestrand, which contained only a single m1. The lighter body mass at Boxgrove, below the 21.5Kg threshold (in contrast to Westbury) may indicate that differences in prey choice occurred (see section 6.3). It is interesting that differences in mass were found between Westbury and Boxgrove, since they are close in age and it is unfortunate that the confidence intervals for Boxgrove were so high. As discussed, variation in size may have arisen from the episodic differences in climate between both sites, leading to changes in prey composition and engendering a relatively rapid response in body size, although sample size is too small to address this possibility.

However, since Britain was connected to mainland Europe during this time, *C. mosbachensis* would have been able to move away from less favourable environments during climatic deterioration phases. This may, in itself, have promoted more stable body mass by allowing *C. mosbachensis* to follow its prey into refugia.

It is also of note that the individual from Sidestrand, which is most similar in age to Boxgrove, had longer m1L in comparison, with more similarity to Westbury m1L. Hence, if m1L is used as a basic proxy for body size, Sidestrand may have been of similar size to individuals at Westbury. It is entirely possible that as well as considerable climatic complexity during this period, there was also a certain amount of regional variation across southern England but the sample sizes are too small for this to be investigated.

The smaller size of *C. mosbachensis* at Boxgrove is, however, similar to other canids from Petralona Cave, Greece and L'Escale, France (Chapter 5.1, Figure 5.60), which have been attributed to the southern European *C.* aff. *arnensis* (Rook and Torre, 1996b). A record of this putative 'southern' species in northern Europe would be surprising and the validity of this species is discussed further in section 6.4.

Material from sites of post Anglian (MIS 12) late Middle Pleistocene age are limited by low numbers of individuals, combined with a lack of material for body mass prediction. Although based on limited material from MIS 11 in mainland Europe, *C. mosbachensis* does

not appear to be gradually increasing towards the much larger size of *C. lupus* after MIS 12. In fact, a slight decrease in size is implied at Monte Zoppega, although without additional data, this is difficult to quantify further.

Thus, although comparisons of *C. mosbachensis* over the breadth of their chronological range were similar, indicating relative constancy in size from the late Early Pleistocene into the Middle Pleistocene, slight variation is present, perhaps the result of regional differences. As discussed, long-term temperate climatic conditions may have fostered initial stability in body mass in *C. mosbachensis* during the Early Pleistocene, which perhaps began to be disrupted by the episodic climatic fluctuations and changing carnivore guild in the Middle Pleistocene (see section 6.3).

6.1.2.3. Body mass estimation of Pleistocene *Canis lupus*

Although *C. lupus* is extant, body masses for Pleistocene representatives were reconstructed to examine whether any large fluctuations in size were a feature of the past, either temporally or spatially. Unlike the other extinct Pleistocene canids, *C. lupus* has a known body mass range at the present day, and thus estimations of mass for the Pleistocene wolves could be directly compared to their modern counterparts. Modern *C. lupus* was used to create the predictive body mass model and it was therefore possible to compare how well the model predicted the actual body mass for *C. lupus* using the %PE.

The mean body mass for modern *C. lupus* entered into the model was 41.33Kg. However, when the regression equation was applied, a mean body mass of 36.35Kg was predicted (with detransformation bias correction factor applied). A %PE of 14.39% was calculated for the species (as the %PE for the equation overall is based on the average %PE of all species used to create the model), indicating an underestimation of modern body mass by 14.39%, which was not far removed from the overall equation %PE of 17.41.

Even though m1L was identified as positively allometric, the predictive equation is still underestimating body mass for *C. lupus*. As modern *C. lupus* was the largest canid present in the study, it is possible that underestimations in the model are caused by the majority of extant canids being smaller in size. Thus, this may have affected the model's ability to predict body sizes in larger canids.

The mean body mass of Pleistocene *C. lupus* from Britain and mainland Europe was estimated at 35.81 ± 1.59Kg (for Britain: 36.25 ± 1.59Kg, for European mainland: 34.23 ±

1.64Kg). Even taking into account the individual %PE for *C. lupus* and consequent underestimation in body mass, Pleistocene *C. lupus* were still smaller than their modern counterparts. The estimated Pleistocene body masses are all within the range of recent *C. lupus* body mass variation (18-80Kg) and it is likely that Pleistocene *C. lupus* demonstrated similar flexibility in body mass, as reflected in the wide variation seen in modern *C. lupus* today.

Both recent and Pleistocene *C. lupus* are above the 21.5Kg dietary threshold, indicating an ability to hunt large prey, as is equally seen in their modern ecology. On this basis, it seems Pleistocene *C. lupus* was likely ecologically similar to its modern counterpart and targeted similarly large prey.

6.1.2.3.1. Palaeoclimatic and palaeoenvironmental implications

Body mass was estimated for all *C. lupus* age groups containing predictive material, as well as by site where applicable, providing temporal and regional comparisons. The following sections discuss the body mass estimates by age group, by site for the British and mainland European sites, and evaluate results in relation to the palaeoclimatic and palaeoenvironmental conditions of each period.

6.1.2.3.1.1. Pleistocene Britain

Estimates from late MIS 7 *C. lupus* reflect the body masses of the earliest members of the species in Britain. The mean estimate for late MIS 7 was 34.03 ± 1.73Kg. However, sites of late MIS 7 were only represented by low numbers of individuals. Estimates were possible for Marsworth (32.37Kg), Hutton Cave (33.16Kg) and Bleadon Cave (38.12Kg), although confidence intervals could not be established due to the lack of individuals needed for the calculation. No estimates were possible for Crayford, Ilford and Tornewton Cave (Otter Stratum) due to the presence of isolated lower carnassials only.

In terms of its palaeoclimate context, MIS 7 was the last interglacial period in a succession of temperate climatic stages of the late Middle Pleistocene. As stated previously, the climatic differences between the Early Pleistocene and later Middle Pleistocene were profound, related to the transition from 41Ka obliquity cycles to 100Ka eccentricity cycles causing extreme fluctuations in climate (Lisiecki and Raymo, 2007; Masini and Sala, 2007).

Discrete temperate-climate faunal groupings, identified as Mammal Assemblage Zones (MAZ), were identified by Schreve (1997) for the late Middle Pleistocene, suggesting the presence of three separate post-Anglian interglacials before the Last Interglacial. MIS 7 can be sub-divided into two assemblages: the earlier Ponds Farm MAZ, indicative of temperate, wooded environments and the later Sandy Lane MAZ, indicative of temperate open grassland (Schreve, 2001a).

The diagnostic Ponds Farm MAZ contains white-toothed shrew (*Crocidura* sp.), in association with straight-tusked elephant (*Palaeoloxodon antiquus*), horse (*Equus ferus*), red deer (*Cervus elaphus*), aurochs (*Bos primigenius*) and bison (*Bison priscus*). Limited *C. lupus* material was found in sites attributed to the Ponds Farm MAZ, with the Tornewton Cave Otter Stratum individual perhaps the only representative (and no body estimate possible), although correlation of this deposit is tentative on account of its unusually low diversity assemblage of carnivores and insectivores (Schreve, 2001a) (see Appendix 1.10 for the full species list).

The majority of MIS 7 sites analysed here, however, were correlated with the Sandy Lane MAZ by Schreve (2001a), which contains predominantly open grassland species such as a late morphotype of steppe mammoth (*Mammuthus trogontherii*), a large form of northern vole (*Microtus oeconomus*), combined with the notable absences of fallow deer (*Dama dama*) and narrow-nosed rhino (*Stephanorhinus hemitoechus*). In terms of carnivores, diversity is much reduced in comparison to the early Middle Pleistocene, with *P. leo* highly abundant, occasional *C. crocuta* (especially in open sites), and rare presence of leopard *Panthera pardus* in upland sites such as Bleadon and Pontnewydd Caves. The interactions of these carnivores with *C. lupus* will be discussed in section 6.3.

Within the four post-Anglian interglacials, smaller scale environmental and climatic oscillations were identified, particularly within MIS 11 and 7 (Schreve, 2001b). With reference to MIS 7, faunal turnover suggested that at least two temperate episodes were present within this interglacial (Schreve, 2001a, 2001b; Candy and Schreve, 2007), paralleling the climatic substages defined by Martinson et al. (1987) as MIS 7e, 7c and 7a for the temperate episodes, and MIS 7d and 7b representing periods of climatic deterioration.

From analyses at the site of Marsworth (Lower Channel, correlated with the Sandy Lane MAZ), Candy and Schreve (2007) demonstrated that the main faunal assemblage from the channel fill was most likely deposited during MIS 7a (~209 ka), based on U-series dating of

reworked tufa, which formed during MIS 7e and 7c. Candy and Schreve (2007) therefore considered it likely that the temperate grassland environments of Sandy Lane MAZ also correlated with MIS 7a and they assigned the older Ponds Farm MAZ to MIS 7e or 7c. Thus, the intervening substage of MIS 7b was associated with major climatic deterioration (accompanied by sea level fall and reconnection to the continent), thereby causing the faunal replacement that occurred between the two MAZs (Candy and Schreve, 2007).

As well as the indicators of open grassland in the vertebrate assemblage, pollen analysis of the Marsworth Lower Channel identified abundant grasses, sedges and herbs (Green *et al.*, 1984). Smaller amounts of tree and shrub pollen were also present at Marsworth, consisting of pine (*Pinus*) and spruce (*Picea*), as well as birch (*Betula*), oak (*Quercus*) and willow (*Salix*) (Green *et al.*, 1984; Murton *et al*., 2001). Coleoptera from the Lower Channel produced MCR estimates of 15°C for mean summer temperatures and -5°C for mean winter temperatures (Murton *et al*., 2001), with some indications of continental influence (Green *et al.*, 1984; Coope, 2001).

The site of Crayford records the very end of the MIS 7 interglacial (Schreve, 2001a, 2001b). Here, the identification of freshwater molluscs in the *Corbicula* bed, in particular the abundant *Corbicula fluminalis*, was taken to indicate that southern Britain was warmer than present at the time of deposition (Kennard, 1944). This contrasts with the mammalian evidence from Crayford, where species indicative of cooler, more continental climates are present, such as *Dicrostonyx torquatus, Lemmus lemmus, Citellus citellus, Coelodonta antiquitatis* and *Ovibos moschatus*, although still within the interglacial. In light of this, Schreve (2001b) proposed that mammalian distribution at this time was affected more by vegetation type (steppe-like grassland) than ambient temperature. The presence of these continental species was also considered as further evidence for a reconnection to mainland Europe in the intervening cool period (Schreve, 2001a).

Although the estimated body masses from Bleadon Cave (38.12Kg), Hutton Cave (33.16Kg) and Marsworth (32.37Kg) are all correlated with the Sandy Lane MAZ of late MIS 7, they are evidently not all exactly coeval. Hutton Cave was considered as younger than Bleadon Cave (Currant, 2004) and the Lower Channel at Marsworth (attributed to MIS 7a) may also be younger than Bleadon Cave. On this basis, it seems that a slight decrease in body mass occurred towards the end of MIS 7. This size variation may reflect some aspect of the climatic fluctuations already mentioned. Although there are no absolute dates in support, the slightly older of age of Bleadon Cave posited by Currant (2004) would place the site

closer to the cold conditions of MIS 7b and the period of mainland reconnection. Thus, the transitional conditions and colder climate may have resulted in larger wolves. In terms of faunal assemblage, Bleadon is characterised by a mixed woodland and grassland environment based on the presence of roe deer (*Capreolus capreolus*) and *P. antiquus* as well as *M. trogontherii* and *E. ferus* (see Appendix 1.8 for a full species list).

Larger size at Bleadon may also relate to the re-connection of Britain to mainland Europe during MIS 7b, perhaps introducing larger wolves into Britain from Europe at this time. European wolves of this age will be discussed in the following section.

Following a period of stabilisation, Britain once again became isolated by sea level rise in MIS 7a (Candy and Schreve, 2007), preventing free-mixing of species. This limitation may have had a knock-on effect on wolf body size by constraining species numbers and movements in the relatively smaller area of island Britain.

However, the presence of very abundant lion (*Panthera leo*) at this time dominating the carnivore community is a more likely reason for *C. lupus* to decrease in size. Competition for resources, perhaps combined palaeogeographical restrictions caused by island status, may have led to a rapid response in body size reduction. This will be further discussed in section 6.3.

The mean estimate for *C. lupus* in MIS 6 was 32.18 ±2.70Kg, based solely on individuals from Clevedon Cave (the only site representing the age group). It is of note that this figure is similar to the Late MIS 7 estimates from Marsworth and Hutton Cave, although the MIS 6 estimate is the lightest estimate for any true wolf in Pleistocene Britain. Hence, it is also interesting to note, *contra* the premise of Bergmann's rule, that the MIS 6 wolves were the lightest recorded.

However, since this is based on a single site, the estimate may not be truly representative of MIS 6 as a whole. The relatively small sized *C. lupus* from Clevedon Cave may therefore indicate localised variation, rather than a wider reduction in body size at this time. MIS 6 spans a 60Ka period of the late Middle Pleistocene (190-130Ka BP). The faunal assemblage from Clevedon Cave indicates cold conditions through the presence of a large form of northern vole (*Microtus oeconomus*) and arctic fox (*Alopex lagopus*) (see Appendix 1.14 for the full species list). The generally restricted nature of the assemblage, containing predominantly small mammals, as well as fox (*Vulpes vulpes*), bear (*Ursus arctos*) and horse

(*E. caballus*), was considered by Currant and Jacobi (2011) as evidence for isolation of Britain at this time.

The question of ice extent in Britain at this time is debated and glacial deposits of this period are few, although the Briton's Lane Formation in East Anglia has been assigned to MIS 6 by Hamblin et al. (2005), correlated with the Saalian Glaciation in northwest Europe. However Hoare et al. (2009) have refuted the presence of ice in Norfolk at this time from the lack of glacial evidence in the beach sediments at nearby Morston. Nonetheless, periglacial conditions have been inferred from the sedimentology, although the dating of these deposits is broad, between MIS 6-2 (Hoare *et al.*, 2009).

Hence, although conditions were undoubtedly cold, they may have been more variable and not sustained throughout the 60Ka time period of MIS 6. Again, because there is information from only one site and there is so little known about the detail of MIS 6, it is impossible to know the wider picture of how wolves responded to environmental change at this time.

As with the lighter body mass estimates from Marsworth, Hutton Cave and Clevedon Cave, the mean estimated body mass for the Last Interglacial (MIS 5e) was 33.54 ± 2.70Kg, based on individuals from Barrington and Joint Mitnor Cave. However, due to a lone individual at Barrington, mean body mass was only calculated for Joint Mitnor Cave, yielding an estimate of 33.69 ± 18.5Kg. The large error is a function of only three individuals being present at the site.

The faunal assemblage of Joint Mitnor Cave has been assigned the 'type assemblage' for the Joint Mitnor MAZ of MIS 5e (Currant and Jacobi, 2001). Britain during MIS 5e was characterised by fully interglacial conditions, with the presence of hippopotamus and Coleoptera indicating summer temperatures around 5°C warmer than today (Coope, 2001), and notably, winter temperatures above freezing (Candy *et al.,* 2010). Thus, in comparison to MIS 7, MIS 5e was significantly warmer than the preceding interglacial.

Both the Joint Mitnor Cave and Barrington assemblages indicate a mosaic landscape, with woodland the dominant characteristic (highlighted by the presence of *P. antiquus, S. hemitoechus*, and *D. dama*, see Appendix 1.16 for the full species list) but some open habitats also present, indicated by *P. leo* and *B. priscus*.

It is interesting to note that MIS 5e *C. lupus* is only slightly larger in size than in the late MIS 7 sites (Hutton Cave, Marsworth) as well as MIS 6 (Clevedon Cave). However, the

confidence interval range is still similar to the slightly smaller estimates. Thus, the continuation of smaller size may relate to the continued presence of *P. leo*, as well as increased abundance of *C. crocuta* in the Late Pleistocene, combined with *U. arctos*, acting to constrain wolf size. The relationship between size and community structure will be further discussed in section 6.3.

For the Early Devensian, due to the presence of single individuals at Bacon Hole and Minchin Hole, only a mean body mass estimate could be provided for MIS 5c as a whole. Hence, the mean body mass for MIS 5c *C. lupus* was estimated at 35.20kg, although due to the low number of individuals, confidence intervals could not be calculated. This larger mass in MIS 5c is within the upper range of that calculated for MIS 5e and is suggestive of an increase in size between the Last Interglacial and the early Devensian.

Both Bacon Hole (Unit G, H, I) and Minchin Hole (Unit 7, 8) have been correlated to MIS 5c and the Bacon Hole MAZ (Currant and Jacobi, 2001, 2011) (see Appendix 1.17, 1.18 for species lists). The Bacon Hole MAZ is defined by the occurrence of *Microtus oeconomus*, as well as *Mammuthus primigenius* and *C. capreolus* (Currant and Jacobi, 2001). In terms of environmental conditions, Minchin Hole (Units 7-8) indicate the gradual opening-up of previously wooded conditions, indicated by the presence of *D. dama* and *A. sylvaticus* in unit 7 and their disappearance by unit 8, replaced by *Microtus oeconomus*. In comparison, Bacon Hole (Units G, H, I) reflects mixed woodland and open environments in all units, with *P. antiquus* and *C. capreolus*, *Mammuthus primigenius* and *Microtus oeconomus.* Large carnivores, *P. leo* and *C. crocuta*, were present (see section 6.3). Although conditions are considered by Currant and Jacobi (2001) to be temperate, these faunas have lost the most thermophilous elements seen during MIS 5e, such as hippopotamus.

Unfortunately, without body mass estimates from the sites, size variation within MIS 5c is difficult to define. Based on their geographical proximity on the Gower Peninsula in south Wales, it is possible that both populations overlapped at times, which would suggest perhaps more similarity. However, without further data becoming available, this remains conjecture.

The slight increase in size in MIS 5c may relate to more favourable, open environment conditions for the cursorial predator in comparison to the more wooded environments of MIS 5e. However, as late MIS 7 was also characterised by open grassland conditions, albeit under a different climatic regime, and a size increase was not evident in wolves, any

increase in size may reflect a different parameter, such as differences within prey abundance and the carnivore community (see section 6.3).

For MIS 5a, mean estimated body mass was 39.85 ± 1.64Kg, indicating that this age group had the largest body mass of any Pleistocene wolf in Britain. However, due to only isolated individuals being present in Bosco's Den, Steetley Quarry Cave, Stump Cross Cave, Windy Knoll and Wretton, only body mass estimates were possible for the larger assemblage from Banwell Bone Cave, with an estimated 39.24 ±0.65Kg for the site.

Banwell Bone Cave has the largest body mass estimate out of all the British Pleistocene sites, and the relatively high number of individuals present (n=13) allows a more precise range of the estimate, which lies close to the modern *C. lupus* mean of 41.33Kg. Although following the trend in increasing body size over the Last Interglacial, this much larger body mass estimate represents a considerable increase in size compared to MIS 5c. Banwell itself was established as the type assemblage for the Banwell Bone Cave MAZ (Currant and Jacob, 2001, 2011) of MIS 5a (Gilmour *et al*., 2007), which is defined by a characteristically low diversity faunal assemblage including *B. priscus* and *R. tarandus*, mountain hare (*Lepus timidus*) and *M. oeconomus*. Smaller carnivores such as *V. vulpes*, *A. lagopus* and wolverine (*Gulo gulo*) are present, with the only other larger carnivore a very large form of *U. arctos* (Currant and Jacobi, 2001). It is particularly interesting that both *P. leo* and *C. crocuta* were absent from the assemblage, which will be discussed in section 6.3.

The Banwell fauna is indicative of cold open environment conditions from the restricted nature of the assemblage, as well as the presence of typical tundra species. From studies of Coleoptera and pollen at the late MIS 5a site of Cassington, the prevailing environment was one of cold, open tundra with palaeotemperature reconstructions based on beetle assemblages typically reconstructing mean summer temperatures of 7 to 11°C and winter temperatures of -10 to -30°C in Britain (Maddy *et al.*, 1998). This was complimented by the pollen assemblages, with a predominance of herbaceous pollen characteristic of Arctic steppe environments dominant (Maddy *et al.*, 1998).

Some evidence of pine was present, although it was considered as unclear by Maddy et al. (1998) whether this pollen was transported in, or represented localised pine trees. The plant macrofossils at the MIS 5a correlated site of Isleworth were also indicative of herbaceous vegetation, although with a lack of tree pollen used as evidence for a treeless environment (Kerney *et al.*, 1982). However, it is worth noting that these more severe conditions were not representative of the entire MIS 5a assemblage at Cassington, where

progressive deterioration in the climate is indicated, decreasing from cool temperatures of 14°C in summer and -4 to 4°C in winter earlier in the assemblage (Maddy *et al.*, 1998).

Nonetheless, severely cold conditions were likely present at Banwell, based on the faunal assemblage. This, combined with the lack of other large carnivores (except for a very large form of brown bear), were very likely responsible for the substantial increase in size of *C. lupus*. Although this increase still fits within a general increasing size trend into the Devensian, it seems to have been more profoundly influenced by the harsh environmental conditions and thus driven by Bergmann's rule (see section 6.1.5). The lack of carnivores of an immediate size class above size *C. lupus* would also have had an effect, which will be discussed further in section 6.3.

In contrast to MIS 5a, the mean body mass estimate for the Middle Devensian (MIS 3) wolves was lighter at 35.40 ±1.63Kg, comprised of individuals from Kents Cavern (Cave Earth) (34.69 ±2.70Kg), Oreston Cave (33.38 ±2.09Kg) and Paviland (37.44 ±2.09). However, due to low numbers of individuals, only an estimate without confidence levels was calculated for Pin Hole Cave (32.42Kg), whilst estimates were not possible for Sandford Hill due to only one individual being represented.

Only the uppermost range of body mass recorded at Paviland approached the sizes encountered during MIS 5a, whereas the other estimates form Kents Cavern, Oreston Cave and Pin Hole Cave are more similar in size to those from MIS 7-5c.

In terms of climate, all body mass estimated sites have been correlated to the Pin Hole MAZ, which has been correlated with MIS 3 (Currant and Jacobi, 2001). This characteristic fauna contains more open environment indicators such as *Mammuthus primigenius, E. ferus,* woolly rhinoceros (*Coelodonta antiquitatis*) as well as *D. torquatus*, *Microtus oeconomus* and hominins. Carnivores present include abundant *C. crocuta, P. leo* and *U. arctos*, the interactions of which with *C. lupus* will be discussed in section 6.3.

The characteristic association of species is indicative of 'Mammoth steppe' conditions. From biological evidence at the MIS 3 site of Lynford (Schreve, 2006), plant macrofossils revealed a cool open grassland of herbaceous plants, with birch or scrub also present, as well as low shrubs of bilberry and crowberry (Boismier *et al.*, 2003). This cool climate vegetation correlated well with the beetle assemblage present, with inferred mean July temperatures of 12-14°C and mean winter month temperatures at or below -10°C (Boismier *et al.*, 2003). More recently, from analysis of coleopteran and chironomids at the

MIS 3 site of Whitemoor Haye, palaeotemperature estimates using the MCR method were suggestive of cooler mean July temperatures of 8-11°C and mean December temperatures of -22 and -16°C (Schreve *et al.*, 2013).

Thus, although in comparison to MIS 5a, climatic conditions had ameliorated, conditions remained cool. It is therefore interesting that even though conditions were slightly warmer overall in MIS 3, *C. lupus* body size had reduced (albeit with great variation), with some sites in line with late MIS 7 estimates. Nonetheless, the larger Paviland estimate is more comparable to the MIS 5a wolves and is in keeping with the increasing body size trend in the Devensian.

It is possible that the large size variation in MIS 3 *C. lupus* may relate to regional differences, with the largest wolves situated in south Wales and the smallest in northern England (see section 6.1.3), or more likely that the variability reflects the extreme, rapid and abrupt climatic oscillations that characterise MIS 3. It is equally possible that the increase in prey diversity relative to MIS 5a, as well as the re-appearance of *P. leo* and *C. crocuta* and the abundance of humans, caused a size decrease in *C. lupus* through competitive interaction, which will be discussed in section 6.3.

Only estimates of mean body mass were possible for MIS 2, since both Cae Gwyn Cave and Ogof yr Ychen were represented by lone individuals. Mean body mass was estimated at 38.57kg, although confidence intervals were not calculated due to the low number of individuals. Even though this estimate is based on limited data, the increase in size to proportions similar to MIS 5a is of note. Based on radiocarbon age estimates from both sites (a *C. antiquitatis* scapula at Ogof yr Ychen estimated as 22, 350±620 Ka BP [van Nedervelde *et al.*, 1973], and a *M. primigenius* carpal at Cae Gwyn Cave estimated as 18,000 +1.4, -1.2 Ka BP [Rowlands, 1971]) (Appendix 1.32 for the full species list), both sites are likely to fall within the period of the Last Glacial Maximum (LGM), the Dimlington Stadial in Britain, correlated to 26-13 ka (early MIS 2) (Rose, 1985). However, both age estimations are subject to error as they were obtained prior to the use of the ultrafiltration method in radiocarbon dating, which better removes contaminants (Jacobi *et al.*, 2009).

Both Cae Gywn Cave and Ogof yr Ychen have been dated to the interval characterised by the Dimlington Stadial MAZ (Currant and Jacobi, 2011) of early MIS 2 (26-13 ka). This MAZ is characterised by the presence of humans (although not recorded at Cae Gywn or Ogof yr Ychen themselves), as well as *R. tarandus*, *C. antiquitatis* and saiga antelope (*Saiga tatarica*) (Currant and Jacobi, 2011), the last not reported at either cave.

Both cave assemblages are indicative of more mixed environmental conditions, although some cool environment indicators are present. Nonetheless, this period is generally characterised by cold open steppe conditions particularly from the presence of *S. tatarica* (Currant, 1987; Currant and Jacobi, 2011). In terms of palaeotemperature, LGM beetle assemblages were dominated by arctic and alpine species indicative of cold, glacial conditions (Coope, 1979), indicating cold conditions for the Dimlington Stadial MAZ. However, climatic conditions fluctuated after the LGM, with brief warming during the Lateglacial or Windermere Interstadial (13-11 ka). By 11 ka, (Loch Lomond Stadial or Younger Dryas), assemblages of arctic/alpine species return, indicating glacial conditions, in particular a mean July temperature cline of 10°C in southern Britain to 9°C in northern Britain (Coope *et al.*, 1977).

It is interesting that the wolves recorded at Cae Gwyn Cave and Ogof yr Ychen are much larger in size than the MIS 3 wolves from Kents Cavern, Oreston Cave and Pin Hole Cave, which may reflect the comparatively colder conditions present during the Dimlington Stadial. Thus, Bergmann's rule may have been in operation, influencing the increase in size due to the colder conditions (see section 6.1.5). However, it is also possible that regional influence had an effect, as like the largest MIS 3 wolf from Paviland, south Wales, the largest MIS 2 wolves were also from south and central Wales. Thus rather than an overall increase in size during MIS 2, western Britain may have had regional environmental and hunting conditions that supported larger wolves.

In relation to a regional effect, although both *P. leo* and *C. crocuta* were present in the MIS 2 sites (as well as during MIS 3), it is possible that these carnivores were locally more scarce in Wales, and hence did not provide as high levels of competition as in the MIS 3 sites characterised by smaller mass estimates. However, without further data from regionally diverse sites of MIS 2 age, it is difficult to quantify this theory.

Nonetheless, it seems that the increasing size trend of *C. lupus* body mass continued into the latest Pleistocene, regaining a size similar to that seen during MIS 5a. Thus, the overall increase in size during the Devensian may correlate with the increasingly intense climatic shifts towards the terminal Pleistocene over time encouraging increasingly large size. However, the increase in size in MIS 2 was likely due to a slightly different set of influential factors than those found in MIS 5a, with both Cae Gwyn Cave and Ogof yr Ychen containing higher species diversity, including other large carnivores.

Pleistocene Britain summary

Overall, a general trend of *C. lupus* increasing in size is present from the Last Interglacial into the Devensian. In particular, MIS 5a *C. lupus* was the largest, followed by MIS 2, and including the estimate for Paviland of MIS 3. In comparison to modern *C. lupus*, which were larger than their Pleistocene counterparts, only those from MIS 5a were comparable in size. Thus, the increasing size trend into the Devensian continued into modern times, resulting in the much larger wolf present today.

However, this view is in contrast to Kurtén (1968), who considered that recent postglacial wolves were smaller than those of the Late Pleistocene. It is also in contrast to the hypothesis by Turner (1981) that the wolves of the Last Interglacial (Ipswichian) were possibly larger than their Devensian counterparts based on tooth dimensions. In a similar study of Late Pleistocene spotted hyaena from Britain, Turner (1981) considered that the increasingly large dental proportions between the Ipswichian and Devensian, combined with a lack of evidence for increasing size in the postcranial skeleton, were indicative of changes in diet rather than body size.

From the comparisons of postcranial material in Britain (section 5.1.6), a larger postcranial size for MIS 5a is suggestive based on lengths of humeri and tibia compared to MIS 7 and 5e. However, due to very limited material, further inferences were not possible, rendering size estimates wholly on teeth as earlier discussed. Thus, although it is suggestive that MIS 5a *C. lupus* were overall larger in size, it is equally possible that following Late Pleistocene hyaenas, *C. lupus* also exhibited increasing dental proportions as opposed to increasing size.

Turner (1981) considered that the increase in dental proportions in hyaena related to dental function, with an increase in size of prey postulated as a causal factor, as well as an increase in harsher climatic conditions. Hence, larger teeth were required for ripping through tougher skin and increasingly thicker fur/hair in order to gain access to carcasses (Turner, 1981). This theory is of note, and more postcranial material would be needed to fully compare whether dentition and postcranials are increasing synchronously, which is unfortunately lacking at this time. Following this, the diet of *C. lupus* will be discussed in section 6.2, as well as in combination with body size in section 6.3.

Nonetheless, the estimated size difference of MIS 5a *C. lupus* is exceptional compared to the rest of the Late Pleistocene, and was within range of recent *C. lupus* mean body mass

(41.33Kg) unlike the other estimates. In contrast, all other estimates were within confidence interval range of each other indicating a more gradual size change over time. Relatively high levels of variation were present in numerous coeval sites, including those of MIS 3 being lighter than expected, as well as a large estimate for Bleadon Cave in MIS 7.

Body mass was also estimated for *C. lupus* present in mainland European sites in Germany and Italy, which are discussed in the following section.

6.1.2.3.1.2. Pleistocene mainland Europe

The presence of temporal variation in body size in *C. lupus* was also explored in mainland European material. As mentioned earlier, the estimated mean body mass of *C. lupus* from mainland European sites was 34.23 ± 1.64Kg. This falls within range of the British Pleistocene estimate, indicating no difference between the two groups. The slightly lighter estimate of body mass may, however, be artefact of the comparatively low numbers of individuals present in the European sites examined.

As stated previously, the dating of many of the mainland European sites used in the analysis is unfortunately not as refined as those in Britain, making correlation to individual climatostratigraphic episodes or marine oxygen isotope stages not possible for the majority of sites. Thus it was necessary for broader age groups to be established, splitting each division of the Pleistocene (Early, Middle, Late) into three further sub divisions (early, middle, late).

Age group 3 (late Middle Pleistocene) is the broad correlative of MIS 7 and 6 in Britain. A mean body mass of 30.65 ± 18.5Kg was estimated, with large range in confidence intervals reflecting to the low number of individuals present.

Due to the lack of precise range for this estimate, it is difficult to compare it to the British estimates for MIS 6 and 7. Nonetheless, this mean value for the mainland European group is suggestive of the lighter body masses also found for MIS 6 (32.18 ±2.70Kg) and 7 (34.03 ± 1.73Kg) in Britain. Regional comparisons will be discussed further in section 6.1.3.

The estimated mean body mass at Weimar-Ehringsdorf was calculated as 31.46Kg, however, no confidence intervals could be calculated due to low number of individuals. Body mass could not be estimated for Dobelhaldeschacht as it contained only a lone individual.

Unfortunately, climatic inferences in northwest mainland Europe during the late Middle Pleistocene, MIS 7 in particular, are limited based on sparse pollen records and lack of robust geochronology of sites (Candy and Schreve, 2007). Hence, the position of an interglacial period between the MIS 11 Holsteinian (Hoxnian in Britain) and the Eemian interglacials (Ipswichian, Last Interglacial) is unclear on the European mainland (Turner, 1998) in contrast to Britain.

In terms of cold stages, in mainland Europe, the Saalian (or Riss) glacial period, situated between the MIS 11 Holsteinian (Hoxnian) and Eemian interglacials (Ipswichian, Last Interglacial) was characterised by multiple 'Saalian' glacial phases creating fluctuating climatic conditions in central and northwest Europe (Busschers *et al.*, 2008). In the Netherlands, the Drente glaciation has been correlated with MIS 6, at which time the Saalian Ice Sheet reached its most southerly limit in the Netherlands (Busschers *et al.*, 2008). Thus, central Europe during MIS 6 was likely cold, with a tundra environment.

Focussing on MIS 7, both the upper and lower travertines present at Weimar-Ehringsdorf have been correlated to late MIS 7 and the Sandy Lane MAZ (Schreve and Bridgland, 2002), with the changes in mammalian fauna between the travertines representative of the climatic oscillations within MIS 7 as discussed in Britain. However, unfortunately, the predictive wolf material does not bear information as to which travertine deposit it came from (R.-D. Kahlke, pers. comm.).

The successive changes in fauna at Weimar-Ehringsdorf correlate well with those observed in Britain at Marsworth (Candy and Schreve, 2007), with woodland favouring species present in the lower travertine, changing to open grassland species by the upper travertine. Hence *P. antiquus* present in the lower travertine is replaced by *M. primigenius* in the upper travertine, as well as the forest adapted *S. kirchbergensis* gradually replaced by grassland favouring *S. hemitoechus* in the mid-lower travertine. The upper travertine also marks the appearance of *C. antiquitatis*, complimenting the predominance of open environment favouring species.

As mentioned, although there are limited records indicative of climate during this period, the presence of travertine formation is a useful indicator of warm interglacial conditions present at Weimar-Ehringsdorf, as formation in Britain only occurs under fully interglacial conditions (Candy and Schreve, 2007). As the majority of wolf material has no designated stratigraphy (save for a skull, which was not used in body mass estimations), it is not

possible to differentiate whether they lived in the more wooded or open grassland conditions represented.

The mean estimate for Weimar-Ehringsdorf (31.46Kg) is similarly light as the estimates from Hutton Cave (33.16Kg) and Marsworth (32.37Kg) and MIS 6 Clevedon Cave (32.18 ±2.70Kg) in Britain during the late Middle Pleistocene. As discussed, the smaller sizes in Britain during late MIS 7 were proposed as relating to stabilising conditions and re-isolation. However, this lighter estimate from central Europe during this time refutes the idea of isolation causing smaller sizes in *C. lupus*. It also potentially contradicts the idea that *C. lupus* was larger in Europe during MIS 7, although this is based on limited data.

Nonetheless, it remains possibly that the complex climatic oscillations of MIS 7 present in both Britain and at least in Weimar-Ehringsdorf, were responsible for body size variation in *C. lupus*.

It is unfortunate that further material, as well as more detailed site information, were not recovered for Dobelhaldeschacht, or in fact any other late Middle Pleistocene sites, which would potentially reveal whether body sizes fluctuated in mainland Europe at this time, or whether the smaller sizes at Weimar-Ehringsdorf were a local variation.

Age group 2.8 (early Late Pleistocene) is the broad equivalent to MIS 5e-a in Britain and has a mean estimated body mass of 34.51 ± 1.76Kg, based on individuals from Bad Canstatt (Villa Seckendorf), Taubach and Monte Tignoso. This estimate is more in line with those of MIS 5e (33.54 ± 2.70Kg) and 5c (35.20Kg) in Britain, and is substantially lighter than MIS 5a (39.85 ± 1.64Kg).

Body mass estimates by site was only possible for Bad Canstatt (Villa Seckendorf), calculated as 34.85 ± 1.90Kg. Both Taubach and Monte Tignoso are represented by lone individuals and estimates were consequently not possible.

However, precise dating of the site is lacking, with an early Devensian age suggested based on correlation with the Untertürkeim travertines positioned opposite the site, and a possible intermediate age between MIS 5e and 5c (Wenzel, 1998). On the basis of faunal comparison, the Bad Canstatt (Villa Seckendorf) mammalian assemblage was also correlated to an early Devensian cold stage by Ziegler (1996), based on the presence of *A. terrestris, L. lemmus* and *Dicrostonyx* (see Appendix 1.47 for a full species list).

The presence of *M. primigenius, C. antiquitatis, R. tarandus* and *B. priscus* all indicate open environment conditions, although some wooded areas may also have been present from the occurrence of *C. capreolus*. From the southwest German Füramoos pollen record (Muller *et al.*, 2003), Early Devensian vegetation changes were rapid, alternating between tundra steppe, pine forest, and deciduous trees reflecting large fluctuations in climate. In particular, MIS 5d was dominated by tundra steppe vegetation, which was replaced by spruce (*Picea*) and eventually by thermophilus deciduous trees in MIS 5c. However, as temperate conditions declined, pine (*Pinus*) became dominant, as well as hardy herbaceous plants of *Artemisia*. Eventually within MIS 5b, a major spread of deciduous trees of *Betula* occurred, as well as an increase in steppe biomes from the high percentages of *Artemisia* plants. During MIS 5a a similarly cyclical re-immigration of *Picea* and deciduous trees occurred, followed by *Pinus* replacement and high levels of *Artemisia* into the steppe biome (Muller *et al.*, 2003). Thus, from the presence of woodland mammalian species in Bad Canstatt (Villa Seckendorf), it seems like mid-substage conditions were reflected. The quick succession of climatic change within each stage likely affected wolf body size, with the fast changes in vegetation affecting herbivorous prey.

The larger size of these wolves in comparison to the late Middle Pleistocene perhaps relates to the quick succession in climatic conditions. However as mentioned previously, as only one site estimate was possible for this broad age group, it is difficult to determine whether the change in body size was just localised, or whether it was part of much larger size variation.

Age group 2.4 (middle Late Pleistocene) is congruent with MIS 3 in Britain, with an estimated mean body mass for age group 2.4 as 36.00 ± 2.70Kg, comprised of individuals from Perick Cave and Ranis. This estimate is similar to that derived for MIS 3 wolves in Britain, and it is possible that similar environmental conditions, combined with the presence of a landbridge between Britain and mainland Europe at the time, may have increased free movement and mixing between species, which will be further discussed in section 6.1.3.

Body mass estimates were not possible for Ranis, which yielded only a lone individual. For Perick Cave, an estimate of 36.66 ± 18.50Kg was made, with the large error recognising the low number of individuals present at the site. This estimate fits well with the rather wide

variation present in British sites of MIS 3 age, especially with the estimate from Paviland (37.44Kg).

The fossiliferous bone gravel of the cave has been correlated to the Weichselian (=Devensian) (Dietrich, 2009), and the faunal assemblage shares affinities with those of MIS 3 with predominantly open environment indicator species such as *R. tarandus*, *M. primigenius* and *C. antiquitatis*, as well as *E. ferus* and European ass (*Equus hydruntinus*) all present (see Appendix 1.50 for the full species list). The cave also contained *P. leo* and *C. crocuta*, and their competitive interactions with *C. lupus* will be discussed in section 6.3.

The cave's position in northwest Germany may mean it experienced a similar vegetation history to that recorded in the Netherlands during the late Weichselian. There, variation between open tundra and steppe prevailed from the presence of steppe herbs such as *Artemisia*, Chenopodiaceae, buttercup family (*Thalictrum*) and *Pinus*, as well as more temperate favouring shrubs/trees such as *Betula* and *Juniperus* (Zagwijn, 1989).

Thus *C. lupus* of this age group likely inhabited cold to cool steppe environments, not dissimilar to those of Britain during this time. Although based on limited comparative European material, the Perick Cave estimate being similar to those of Paviland is interesting and perhaps indicates similar conditions between the sites, which will be discussed in section 6.1.3.

Age group 2 (late Late Pleistocene) is congruent with MIS 2 in Britain, although an estimate of body mass was not possible for the continental age group 2, since the only site present, Grotta di Paglicci, contained a single individual.

Pleistocene mainland Europe summary

Although based on limited evidence, Pleistocene *C. lupus* from mainland Europe also shows an increasing body size trend into the Late Pleistocene in similarity to Britain. However, comparisons with coeval mainland European sites were problematic, rendering inferences on whether the size represented local variation rather than representing the size of the age group impossible. Nevertheless, regional comparisons with Britain will be discussed further in section 6.1.3.

It seems that following Britain, the increasing body size trend may relate to the intensification and frequency of climatic shifts, with increases in size incremental with each transition. However, differences in carnivore community structure and prey abundance may also have an influential effect on body size, which will be discussed in section 6.3.

6.1.2.4. Summary: Temporal differences in body size: palaeoclimatic and palaeoenvironmental implications

In summary, the mean body mass of Pleistocene *C. lupus* from Britain and mainland Europe (35.81 ±1.59Kg) is within range of the body mass variation of its modern counterpart. Regarding the Pleistocene canids, *C. lupus* is the heaviest, and hence largest, canid present during the late Middle to Late Pleistocene, with *C. mosbachensis* lighter and hence of smaller size (22.50 ±1.62Kg). The mean body mass estimate for *C. etruscus* (24.34 ±1.65Kg) is slightly heavier than that of *C. mosbachensis*, although with some overlap in the confidence interval range of the estimate. The body mass estimate for *C. arnensis* (17.94 ±1.73Kg) reveals that it is the lightest, and hence smallest, of the Pleistocene canids analysed here, being just over half the size of Pleistocene *C. lupus*.

Variation in size between Olivola F.U. and Tasso F.U. *C. etruscus* may relate to changes in carnivore competition (see section 6.3), since climatic differences between the sites were minimal.

Although body size in *C. mosbachensis* was relatively stable from the late Early Pleistocene of Untermassfeld to the MIS 13 site of Westbury sub Mendip, size fluctuated more by the later MIS 13 Boxgrove, and post Anglian/Elsterian glaciation of MIS 12 in European sites. Hence, increased climatic deterioration towards the Middle Pleistocene may have caused variation in otherwise previously stable body mass. However, changes in the carnivore community during the Middle Pleistocene may have also been responsible (section 6.3.).

In contrast, Pleistocene *C. lupus* had more temporally variable body masses than the other Pleistocene canid species analysed. An increasing body size trend is evident into the Devensian, potentially coinciding with further deterioration of the climate towards the Last Glacial Maximum and the terminal Pleistocene. Variation in size by site were common within an age group, which may reflect climatic oscillations for MIS 7 wolves, or perhaps regional differences for MIS 3 wolves (discussed in section 6.1.3).

Changes in the body size of mammals are a relatively common ecophenotypic response to changes in climate and environment (Reynolds, 2007), and are exemplified by the size variation within *C. lupus*. As discussed, all the Pleistocene body mass estimates and their variations are within the body mass range of recent *C. lupus*, highlighting the flexibility of *C. lupus* and enabling the species to cope with environmental change. This coping mechanism is evident by its continued presence throughout the Pleistocene, whilst the comparative inflexibility to climate change of both *C. etruscus* and *C. mosbachensis* may have ultimately contributed to their disappearance.

6.1.3. Regional effects on body mass

Regional differences between populations of mammals may arise from geographical barriers such as mountains, or by more relatively ephemeral barriers such as glaciers. Differences in climate regionally may also affect body mass in relation to latitude and Bergmann's rule, which will be discussed in section 6.1.5.

The analysis of regional differences was not possible for *C. etruscus* and *C. arnensis* due to lack of comparative sites, whilst for *C. mosbachensis* limitations were related to lack of Early Pleistocene material in Britain, as well as low numbers of individuals. Regional comparisons were possible for *C. lupus*, although problems existed relating to less precise age correlations for the mainland European material, as well as low numbers.

6.1.3.1. Palaeogeographical isolation of Britain from the continent and regional differences

As discussed in relation to temporal variation and climatic influence, many of the body mass estimates for Pleistocene *C. lupus* varied by site, although generally all overlapped in their confidence interval ranges (excluding MIS 5a). The presence of variation between these sites, and especially within the same age group, raises the question of whether regional differences are influencing body size. This section will therefore discuss the presence of regional differences in age groups in Britain, as well as the effect of isolation from the continent.

Over the course of the Pleistocene, Britain has fluctuated from being a peninsula of mainland Europe, to being an island. During the Early Pleistocene, Britain was permanently connected to the mainland by a landbridge (the Weald-Artois Anticline), together with low

global sea levels (Funnell, 1995). However, by the start of the late Middle Pleistocene, a combination of North Sea basin subsidence, eustatic sea level rise, and the breaching of the Chalk anticline during the Anglian glaciation, led to the formation of the Strait of Dover (Funnell 1995; Keen, 1995), thereby isolating Britain from the mainland during periods of warm climatic conditions with high sea levels.

The ensuing Middle and Late Pleistocene cold periods, characterised by high ice volume and associated lowered sea levels, repeatedly reconnected Britain to the mainland by a broad northwest European land mass (now the southern North Sea basin) (White and Schreve, 2000). Similarity in fauna across northwest Europe during these times provides key evidence for passage between Britain and mainland Europe.

Thus, prior to the Anglian glaciation of MIS 12, similarities in fauna between Britain and Europe would be expected, however after this, more differentiation would be expected during interglacials because of Britain's climate-driven isolation.

Evidence of isolation of Britain followed by reconnection can be seen in Britain during MIS 7, based on the dramatic mid-interglacial faunal turnover from temperate woodland faunas of early MIS 7 to the equally temperate, open grassland fauna (Schreve, 2001a, 2001b). As discussed earlier, although predominantly an interglacial period, MIS 7 is characterised by three temperate episodes (MIS 7e, 7c and 7a) interspersed with evidence for cold conditions during MIS 7d and 7b (Martinson *et al.*, 1987). These cold periods, presumably with associated lowering of sea level, allowed mammals to travel freely into Britain, prior to re-isolation (Schreve, 2001a, b; Candy and Schreve 2007).

As introduced in Chapter 2, the earliest evidence for *C. lupus* in Britain is from late MIS 7, suggesting that the reconnection of Britain at this time allowed the immigration of *C. lupus*, along with other large herbivores, into Britain. Arrivals into Britain at this time included the late morphotype of steppe mammoth, *M. trogontherii*, and *E*. *ferus*, Merck's rhinoceros *Stephanorhinus kirchbergensis*, *P. leo* and *C. crocuta*, albeit in reduced numbers (Schreve, 2001a).

As suggested, this re-connection to Europe may be responsible for the larger size of Bleadon Cave *C. lupus* in comparison to those of the reportedly younger Hutton Cave and Marsworth, based on larger animals being present in Europe prior to this time. However, although based on very limited data, the smaller size of the Weimar-Ehringsdorf estimate is suggestive that late MIS 7 wolves were not all as large.

The reduction of size during late MIS 7 was also proposed above as relating to island isolation in Britain, whereby without free exchange of species, carnivores may have been more constrained in terms of competition as well as in range size. However, the similarly small body mass estimate for Weimar-Ehringsdorf, also of MIS 7, to both Hutton and Marsworth is contradictory, and will be discussed in the following section.

Focussing on Britain, sites of late MIS 7 were mostly from southern Britain, with both Bleadon Cave and Hutton Cave situated in Somerset in the southwest, and Marsworth in Buckinghamshire in the central south, hence only slight regional differences exist, although the southwest sites are in much more elevated terrain.

As Bleadon and Hutton are in geographically similar locations, the differences in body mass may relate more to temporal differences, and perhaps more likely related to the effect of re-connection of Britain to the mainland during MIS 7b as discussed. In contrast, as both Hutton and Marsworth may be similar in age, and are more distant from one another, the closeness in their mass estimates may suggest some regional similarity between the sites.

The coincidence of large sized *C. lupus* with large sized herbivores and open environments is often cited as a causal factor in driving their larger size, compared to *C. mosbachensis*, enabling them to more effectively hunt the larger sized prey. However, the combination of reduced carnivore diversity during MIS 7 was also an important factor, of which both will be discussed in section 6.3.

Britain was probably isolated from the continent during most of MIS 5, based on evidence of raised beaches during MIS 5e (see Keen, 1995), indicative of high sea levels attained during the warmest substage, as well as 5c and 5a, albeit based on more limited evidence. Nonetheless, the mismatch between British and other European faunas throughout this stage (Currant and Jacobi, 2011), such as the notable absence of spotted hyaena during MIS 5a (Turner, 2009), support the proposed isolation of Britain at this time.

However, the association of a cold, low diversity mammalian fauna combined with the presence of more temperate molluscs and Coleoptera (Coope *et al.*, 1997; Maddy *et al.*, 1998) was considered as evidence for a possible re-connection to the continent during the preceding cold sub-stage of MIS 5b by Gilmour et al. (2007) and Currant and Jacobi (2011). The mammalian species, having entered Britain, were subsequently trapped in Britain by rising sea-levels in MIS 5a (Gilmour *et al.*, 2007; Currant and Jacobi, 2011). Renewed isolation may further account for the relative stability and low species diversity in the

mammal fauna during MIS 5a, preventing any subsequent faunal immigration and turnover, as well as for the absence of human activity in Britain (Gilmour *et al.*, 2007; Currant and Jacobi, 2001, 2011).

It is unfortunate that the more numerous northern sites in Derbyshire and Yorkshire of MIS 5a age contain only single individuals, such as Stump Cross Cave, Steetley Quarry Cave and Windy Knoll, as these would have made an interesting regional comparison with Banwell Bone Cave in the south west. As it stands, no regional comparison was possible within Britain for MIS 5a.

During MIS 3, low sea-levels enabled Britain to be reconnected to mainland Europe by a broad landmass in the southern North Sea Basin (Stuart, 1995). The similarity in faunal assemblages between Britain and the continent at this time indicate unimpeded migration of species, and homogenisation of fauna. In particular, the return of Neanderthals to Britain at this time, combined with mammals of the characteristic 'mammoth steppe' community in Britain (Currant and Jacobi, 2001) attest to this re-connection.

During this time in Britain, Pin Hole Cave was the most northerly site (East Midlands) in the data, with a mean body mass estimate of 32.42Kg. The remaining sites were all situated in south west England and south Wales. Both Oreston Cave and Kents Cavern are situated in Devon, and their wolves have estimated mean body masses of 33.38 ±2.09Kg, and 34.69 ±2.70Kg respectively. However, for south Wales, the mean body mass estimates were comparatively larger, with Paviland estimated as 37.44 ±2.09Kg, and 37.14 ±18.5Kg at Black Rock Quarry.

Differences between the southwest of England and south Wales are difficult to quantify. Both are areas of moderate elevation. Nonetheless, these larger sizes are also reflected at the MIS 2 sites of Cae Gywn Cave and Ogof yr Ychen, both situated in south and central Wales. Hence, although based on limited data, it seems western Britain supported larger sizes of wolf.

During the Last Glacial Maximum (MIS 2), Britain was reconnected to the continent, with final isolation of Britain occurring post-LGM, relating to isostatic uplift of Britain due to the unloading pressure of the ice sheet, combined with higher sea-level due to the consequential melt water (Lambeck, 1995).

Overall it is difficult to assess whether north-south or east-west regional differences occurred in Britain, due to lack of data. However, in MIS 3, differences between south Wales and south west England were apparent, although perhaps relating more to smaller scale local variation in environment, prey and competitors, rather than regional scale differences. It is nonetheless compelling that Welsh sites of MIS 2 also contained large sized wolves.

It is therefore difficult to draw any conclusions on regional differences in body mass in Pleistocene Britain. More data are needed, specifically material that allows for use in body mass estimation. Nevertheless, the variation observed highlights that even though general increasing size trends are apparent through time, there is potential regional variation, suggesting that wolves form important local populations.

6.1.3.2. Regional differences in Britain compared to mainland Europe

As discussed, due to a lack of sites containing *C. etruscus* and *C. arnensis*, regional inferences were not possible. In particular for *C. etruscus*, the sites of Olivola and the Upper Valdarno are both from the same region in Tuscany, Italy.

For *C. mosbachensis* and *C. lupus*, a general lack of data renders inferences on regional differences within mainland European sites of the same age as impossible. However, regional comparison between some British and German sites were possible.

C. mosbachensis from the late Early Pleistocene site of Untermassfeld and the early Middle Pleistocene site of Westbury-sub-Mendip were similar in their estimated body masses. Hence, temporal variation in mass was not apparent. This lack of variation is suggestive of regional stability between mainland Europe and Britain during the late Early and early Middle Pleistocene, which based on their geographical separation of approximately 700 miles (1126.54Km), is notable. Over this time period, Britain was connected to mainland Europe providing free movement of species between both regions and potential homogenisation of fauna.

For *C. lupus* from broad age group 3 (late Middle Pleistocene, correlated to MIS 7 and 6), the wolves from the site of Weimar-Ehringsdorf have a mean estimated body mass of 31.46Kg, although lacking in confidence intervals due to low numbers of individuals.

As discussed, both the fossil-bearing upper and lower travertines at Weimar-Ehringsdorf have been correlated to MIS 7 (Schreve and Bridgland, 2002). However, the lower

carnassials used for body mass estimation have no information pertaining as to which travertine they belong (R.-D. Kahlke, pers. comm.).

The body mass estimate for Weimar-Ehringsdorf is similar to those of Hutton Cave (33.16Kg) and Marsworth (32.37Kg) (also without confidence intervals) of MIS 7 in Britain, and was also characterised by broadly similar climatic conditions of temperate open grassland. The similarly light body mass estimates for these sites is suggestive of some regional similarity of conditions between Britain and central Germany during late MIS 7.

However, the heavier estimate for Bleadon Cave (38.12Kg) is not replicated, although the European comparison is based on very limited data. Thus the proposal that larger *C. lupus* initially travelled into to Britain from Europe during reconnection of MIS 7b is difficult to quantify. Although smaller sized *C. lupus* may also have been present in Europe, Weimar-Ehringsdorf may represent localised size variation rather than generally smaller wolves at this time. In particular, sites closer to Britain of this age would be needed to further develop this theory. Equally, Bleadon Cave may also represent localised variation within late MIS 7.

As discussed, the site of Bad Canstatt (Villa Seckendorf), Germany, was assigned to the broad European age group encompassing MIS 5e-a. The site has a mean body mass estimate of 34.85 ±1.90Kg, which whilst it is in range of MIS 5e Joint Mitnor Cave (33.69 ±18.50Kg), is lighter than MIS 5a Banwell Bone Cave (39.24 ±0.65Kg).

Based on the faunal associations at Bad Canstatt, climatic conditions were cold and are thought to date to the early Weichselian (Ziegler, 1996). Ultimately due to the lack of precise dating for the Bad Canstatt (Villa Seckendorf) material, regional comparisons are difficult, with a possible age range spanning 54,000 years (125,000-70,000 ka BP).

Perick Cave, Germany, of broadly MIS 3 age, has a mean estimated body mass of 36.66 ±18.50Kg, which is similar to the estimates from British MIS 3 sites. However, the large confidence interval range makes reliable regional comparisons with Britain at this time difficult as it encompasses all estimates for MIS 3 sites.

Like the British MIS 3 sites, the faunal groupings at Perick Cave are also suggestive of cold, open steppe conditions, indicative of regional similarity at this time related to the connection between Britain and mainland Europe. Interestingly, at Jaurens Cave in southern France, a large wolf has been recently identified as the subspecies *Canis lupus maximus* (Boudadi-Maligne, 2012) on the basis of it being larger than *C. lupus* at other

French localities, as well as extant wolves from western Europe based on dental and skeletal dimensions. Regional variation is therefore apparent within Europe at this time.

A radiocarbon age estimate of 29,300 ±1400 BP and 32,630 +2900, -2100 BP (Boudadi-Maligne, 2012) correlates these wolves with late MIS 3. However, this purported larger sized wolf is not recognised from sites of MIS 3 age in Britain. In contrast, the largest size wolves in Britain were found earlier during MIS 5a.

It seems likely that rather than representing a subspecies of wolf, the individuals from Jaurens Cave may represent a local size variant population, which based on the amount of variation within sites of similar age in Britain, seems probable. From the large range of sites of MIS 3 age examined here, no wolves were of similarly large size to those encountered in MIS 5a. In particular, the mean estimates from Black Rock Quarry and Paviland, although larger than their MIS 3 counterparts, are still lighter than those in MIS 5a.

This comparison exemplifies the importance of local variation. Although regional environmental differences may have been present between Britain and southwest France during MIS 3, the connection between Britain and mainland Europe at this time would have encouraged free movement of species. Thus, similar to the larger wolves of MIS 3 in south Wales, local conditions perhaps engendered larger sizes.

As introduced in Chapter 3, body sizes in latitudinally different regions are potentially influenced by Bergmann's rule, with both temperature and climate differences important variables. However, regional differences may not simply be related to latitude and climate, but may also reflect different prey availability.

The British and mainland European sites analysed here are relatively similar in terms of latitude, climate and environment, and do not display marked regional differences. It would be interesting in future to compare the northern European Pleistocene sites containing *C. lupus* with those from southern Europe, particularly the Iberian and Balkan peninsulas in order to gauge regional change at extreme ends of the range.

Summary

For the majority of the Early to Middle Pleistocene, faunal interchange was able to take place between Britain and mainland Europe, and thus both *C. mosbachensis* and *C. lupus* (at times) would have had increased opportunity to range and establish themselves across both regions. Following brief periods of re-connection, the re-isolation of Britain during the

later Pleistocene, such as during MIS 5b to MIS 5a for example, may have had some effect on size in *C. lupus*. Specifically during MIS 5a, putative island isolation combined with cold conditions had a noticeable effect on body size. However, the lack of comparative mainland European data during this time makes further inferences on the effect of re-isolation in Britain at this time difficult.

Thus, with the exception of Britain during MIS 5a, local variation in *C. lupus* body size is perhaps a more influential factor than fluctuations between isolation and connection between Britain and Europe. Differences in local environment, and changes in prey abundances and other carnivores may therefore be more important variables influencing body size variation, which will be discussed in section 6.3.

6.1.4. Sexual dimorphism in cranio-dental characters of *Canis lupus*

In comparison to felids and other small carnivores such as mustelids, sexual size dimorphism has previously been considered unimportant in canids (Ewer, 1973). More recent studies into sexual dimorphism, such as Dayan et al. (1992), equally found that recent *C. lupus* from Israel were generally less dimorphic than either felids or mustelids, based on comparisons of lower carnassial length, condylo-basal length of the skull and diameter of the upper canine. This result was replicated by Van Valkenburgh and Sacco (2002) who found in a larger study that recent canids were generally less dimorphic than felids based on similar measurements of wild-caught museum specimens (exact localities of specimens not presented).

As fossil material is difficult to separate by sex due to its generally incomplete nature (Dayan *et al.* 1992), the modern European *C. lupus* dataset was used to explore the potential amount of sexual dimorphism present in a subset of the measurements. Contrary to the aforementioned studies, *t* tests found significant ($p<0.05$) differences between the mean male and female measurements. Only m2L was found as non-significant ($p>0.05$) and of less utility in identifying sexual dimorphism.

As outlined in chapter 4, the Coefficient of Variation (CV) examines the variability of each measurement for males and females. Generally, males had higher CVs than females, although variability overall was not dissimilar. The percentage of sexual dimorphism in the same measurements was found to range between 2.27% – 8.02%. Dayan et al. (1992) reported that in modern *C. lupus* from Israel, sexual dimorphism was more pronounced in canine width (6%) than in the lower carnassial (3%) and condylo-basal length of the skull

(3%). In comparison to Israeli wolves, the European dataset was found to be more sexually dimorphic in the lower carnassial (6.94%) and condylo-basal length (4.81%).

Gittleman and Van Valkenburgh (1997) related dimorphism in carnivore canines to their breeding system, with polygamous carnivores such as lions having high levels of dimorphism related to male-male competition and dominance displays utilising canines. In contrast, these authors found that monogamous carnivores, such as canids, had less conspicuous canines that were not as important for display in male-male confrontations. Hence, canids have reduced canine dimorphism related to their monogamous breeding behaviour (Gittleman and Van Valkenburgh, 1997).

Carnassials were found to be less sexually dimorphic than canines (Dayan *et al.*, 1992; Gittleman and Van Valkenburgh, 1997), which may relate to their functional importance in diet rather than in sexual competition. Gittleman and Van Valkenburgh (1997) further found that carnassial dimorphism was only present in carnivores, thus reinforcing the strong relationship between carnassial function and carnivory.

Hence, although recent European *C. lupus* is only relatively slightly more sexually dimorphic in this study than the *C. lupus* from Israel reported by Dayan et al. (1992), it nonetheless raises questions as to the cause behind the increased dimorphism in northern European wolves. It is possible that latitudinal differences between these wolf populations are being reflected, which will be discussed in section 6.1.5.

In terms of gauging the level of sexual dimorphism in the Pleistocene canids, due to the difficulties in separating fragmentary fossil material by sex, sexual dimorphism in *C. mosbachensis, C. etruscus* and *C. arnensis* could not be examined. However, based on the relatively low level of sexual dimorphism in its modern counterpart, Pleistocene *C. lupus* is unlikely to have been more sexually dimorphic.

In an analysis of the exceptionally-well preserved Rancho La Brea specimens of Late Pleistocene North America, Van Valkenburgh and Sacco (2002) found that Pleistocene *C. dirus* exhibited similar levels of sexual dimorphism to recent *C. lupus*. It is therefore suggested that the Pleistocene canids analysed in this research may have followed the canid trend of having generally low-level, but nevertheless present, sexual dimorphism.

6.1.5. The relationship between *C. lupus* and Bergmann's rule

Bergmann's rule states that warm-blooded mammals from cooler climates tend to be larger than their congeners from warmer climates (Bergmann, 1847). The rule was subsequently reformulated to refer to populations within species. Thus, within a given species of homeothermic animal, populations living in colder climates are generally larger than populations living in warmer climates (Rensch, 1938; Mayr, 1963).

In light of this, it was decided to examine whether any latitudinal changes in body size were apparent in the recent *C. lupus* dataset, which extended from 39°N to 67°N over Europe. If Bergmann's rule can be demonstrated in recent wolves, then in lieu of latitudinal differences, changes in size may be relatable to climatic differences during the Pleistocene. Thus cold-climate wolves (correlated with those of high latitudes) may be larger than warm climate (and hence lower latitude) wolves.

Least squares regression however indicated that the relationship between latitude and m1L (used as a proxy for body size) did not fully explain the variation found in the recent *C. lupus* dataset, suggesting the possible presence of other, more influential factors on body size such as differences in carnivore community and competition, as well as prey abundances.

Nonetheless, this proxy for body size indicated that the largest individuals of recent European *C. lupus* were from the high latitudes (60°N) but notably not from the highest latitudinal extent of the data (67°N). Although there are fewer individuals from latitudes >60°N, there seemed to be a slight decrease in size past this latitude.

A similar scenario was outlined by Hersteinsson and Macdonald (1992), whereby although body size in most mammals increases latitudinally up to 60-65°N, species found predominantly north of 60°N such as arctic fox (*A. lagopus*) may trend towards smaller size with further increasing latitude. This was based on the theory that in climatic regions where food resources may be low, such as deserts or tundra, body size of mammals is limited by food supply (Rosenweig, 1968), and hence where resources and diversity are low, larger body sizes are less able to be supported.

In terms of its distribution in the arctic regions of Sweden, *C. lupus* was considered as 'polyzonal' by Callaghan et al. (2004), whereby it was able to inhabit into the arctic zone, but focussed on areas that were more bio-diverse. This likely has some relationship with

the arctic tree line in Sweden, which although highly regionally variable in the Palaearctic, fluctuates around 68°N in Sweden (Bogaert *et al.*, 2011).

The comparatively smaller body sizes for *C. lupus* >60°N may therefore be a reflection of decreasing prey resources towards the sub-arctic regions of Sweden. In particular, migration of herd ungulates such as semi-domestic *R. tarandus*, and perhaps even the seasonal movements of ptarmigan and lemming to escape unfavourable conditions, would limit the diversity and abundance of potential prey (Callaghan *et al.*, 2004). This is certainly the case in high latitude *A. lagopus*, where changes in the abundance of lemmings controls the emigration of the species (Hersteinsson and Macdonald, 1992). However, as suggested, competition from other carnivores such as Eurasian lynx (*Lynx lynx*) and interestingly, from *U. arctos*, may also be an influential factor on body size at high latitudes (see 6.3).

The smallest individuals were from lower latitudes in Europe: from Portugal, Serbia, the Pyrenees and France (for map see Chapter 4, Figure 4.5) and were all female (the significance of this will be discussed in section 6.1.6). However, a few lower latitude European wolves from Bosnia and Spain in particular (both male, discussed in section 6.1.6), were of a similar size to those from high latitude Sweden (>67°N). Generally, only a slight size cline exists over the latitudinal extent of the data and it would therefore be interesting, in a future study, to include more individuals from southern Europe within the dataset.

In light of this, the Middle Eastern subspecies *C. l. arabs* was incorporated into the recent *C. lupus* data in order to examine body size over a larger latitudinal range. The Arabian wolf was considered a reasonable equivalent for low latitude *C. lupus*, since as a desert-adapted subspecies, it extends the range of the species as a whole. The *C. l. arabs* data were from Jordan, Oman and Saudi Arabia, and the results highlighted the presence of a latitudinal size cline, with low latitude *C. l. arabs* much smaller than high latitude *C. lupus*.

Thus, based on analysed data, the wolf family follow Bergmannian size clines. However, although latitude (and hence climate and ambient temperature) appear to be important factors in body size, other aspects such as food resources, competition, as well as altitude may also be having an effect.

As discussed, animals in resource limited environments, such as deserts and tundra were considered by Rosenweig (1968) to be limited in body size due to the lower availability of

food, which may be as true for Arabian wolves as it is for high latitude (>65°N) *C. lupus* in Sweden.

The Arabian wolf inhabits the arid desert and mountains of Israel, Jordan, Syria and the Arabian Peninsula. Based on a study of *C. l. arabs* in the Negev Desert, Israel, the main food resource was refuse from human settlements and carrion, with a small proportion (6.3%) of cape hare (*Lepus capensis*) and small sized Dorcas gazelle (*Gazella dorcas*) found in analysed scats (Hefner and Geffen, 1999). The reliance on human refuse may reflect the lower resources available in terms of mammalian prey and may provide a relatively regular resource of food for the Arabian wolf. Thus, factors other than lower resources may be responsible for the smaller body sizes found in the Arabian wolf, particularly in Israel.

As introduced in Chapter 3, climate, and hence ambient temperature, is an important factor in metabolic rate and temperature regulation in mammals. In comparison with cold climate species, those in warmer climates tend to have lower basal rates (Lovegrove, 2000) and as a result, have comparatively lower energy requirements. Hence, as basal rate scales positively with body mass (Elgar and Harvey, 1987; McNab, 1988, 1990), mammals from warmer climates with lower basal rates tend to be of smaller size.

Temperature regulation in mammals is related to surface area (McNab, 1971), with smaller sized mammals more able to transmit heat (high conductance) more effectively than their larger counterparts. For *C. l. arabs*, Hefner and Geffen (1999) found the monitored Israeli population most active at night, and by day inactive and under cover to avoid day-time heat. Thus, Arabian wolves cope with warmer conditions by being active at night, even though they are more adapted to warmer climates by their size than larger congeners.

The relationship between fur colouration and regulating body temperature is complex, and colouration may relate to other behavioural factors (Walsberg, 1983), such as inter-species communication and sexual selection (Caro, 2005). Colouration also has a relationship with environment, in terms of camouflage based on higher latitude canids having whiter colouration, desert canids being pale, and forest canids generally having dark colouration (Caro, 2005). Thus, colouration may be more of an adaptive response to environmental conditions for camouflage, rather than directly related to warmer climates.

From the *C. l. arabs* dataset, at least four of the nine individuals were from the mountainous region of Al Hajar, Oman (2000m elevation), and the Mountain Heights Plateau, Jordan (600-1500m elevation), or at least were killed there. The relationship

between altitude and body size in mammals is unclear but physiological adaptations to high altitude relating to higher oxygen uptake occur in high altitude mammals such as vicugna (*Lama vicugna*) and alpaca (*Lama pacos*) (Leon-Velarde *et al.*, 1996), for example.

In the Leon-Velarde et al. (1996) study, high altitudes were considered as >4000m, whereby the altitude for Al Hajar and the Mountain Heights Plateau are relatively much lower in comparison. Hence, it is reasonable that smaller sizes of *C. l. arabs* are also not related to the higher altitude some individuals were recovered from. Also, based on range sizes of 34.6 ± 19.5Km^2 in the Negev desert, Arabian wolves would not necessarily be restricted to higher areas (Hefner and Geffen, 1999). Overall, there are limited numbers of *C. l. arabs* used here, and all are lacking in precise elevation data. Nonetheless, it would be very interesting to examine size differences between populations at sea-level and at altitude.

In summary, there is a slight size cline in recent European *C. lupus* with increasing latitude. When this is extended to include low latitude *C. l. arabs*, a Bergmannian response to latitude is more evident. However, a drop-off in size present in the highest latitude (>65°N) Swedish *C. lupus* is perhaps related to limited availability of resources in sub-arctic environments. The same may also be true for smaller body sizes in low latitude desert-adapted *C. l. arabs*, although reliance on human refuse in some populations may counteract the limited prey availability in these regions. The presence of a latitudinal size cline may therefore obliquely relate to climate, with changes in prey abundances influential, as well as the effect of other competitive predators, which will be discussed in section 6.3.

6.1.6. The relationship between latitude and sexual dimorphism in *Canis lupus*

When the modern European wolf dataset was separated by sex, based on m1L as a proxy for body size, males were found to be generally larger than females over all latitudes, with the largest individuals from high latitudes being all male, and the smallest individuals from lower latitudes being all female. In comparison to the slight latitudinal size cline observed, size-related sexual dimorphism seems to have a greater effect.

As discussed in section 6.1.4, sexual dimorphism in *C. lupus* is generally low in comparison to other carnivores, with dimorphism for the lower carnassial calculated as 6.94% between males and females in the recent European wolf dataset. Although dimorphism in the carnassials was found to be related to diet rather than reproductive behaviour (Gittleman and Van Valkenburgh, 1997), m1L was found to be significantly different between males

and females in the modern European *C. lupus* dataset, suggesting that sex-related differences were apparent (assuming that diet between males and females was similar).

When *C. l. arabs* was included with modern *C. lupus* and separated by sex, the dimorphism apparent in the latter was less pronounced in the Arabian wolf. Although this may be an artefact of the low numbers of individuals considered (n=9), it may tentatively explain why lower levels of sexual dimorphism were found in measurements of low latitude Israeli wolves by Dayan et al. (1992), in comparison to the slightly higher level of dimorphism in the higher latitude modern European wolves studied here. This questions the relationship between latitude and sexual size dimorphism. Thus, based on the assumption that m1L is reflecting different male and female body size rather than diet, as body size increases with increasing latitude, does the effect of latitude exacerbate the, albeit slight, sexual dimorphism found in wolves?

For the modern European *C. lupus* dataset, least squares regression explored the relationship between latitude and m1L (in lieu of body size) for males and females separately. The relationship for females was strongly correlated and significant ($p<0.05$), however, for males this relationship was weakly correlated and non-significant ($p>0.05$). Thus male body size is less explained by latitude in comparison to female body size, based on m1L. This suggests that for males, factors other than latitude are important in causing variation in body size.

As discussed in the previous section, latitudinal-related size variation is a function of varying metabolic basal rates, and hence differences in energy requirements, between warm and cold climates, plus the relationship between heat transfer and surface area. However, limited food resources also influence size in both low latitude desert and high latitude tundra environments, as well as the possible influence of competition (section 6.3) indicating further complexity in the relationship between size and latitude.

The influential factors controlling male sexual size dimorphism are similarly complex, whereby, as introduced in Chapter 3, dimorphism is related to a range of factors including sexual selection, parental investment in young and breeding system. This correlates well with Gittleman and Van Valkenburgh (1997) considering that males were not simple proportional enlargements of females, with the factors influencing dimorphism not predictably influencing dimensional changes.

In relation to the differences between males and females, Rensch's rule states that male body size is more variable than female body size among related species (Rensch, 1960). However, as discussed, factors controlling sexual dimorphism such as sexual selection may be the ultimate driver of Rensch's rule (Fairbairn, 1997). Nevertheless, the rule has been upheld to some extent in the modern European wolf dataset here, both using m1L as a proxy for body size, and in the differences in the CV of measurements for males and females.

In a recent study by Blanckenhorn et al. (2006), the relationship between Rensch's rule and Bergmann's rule was explored within 98 species (60 vertebrates, 38 invertebrates). In general, no evidence supported the traditional version of Rensch's rule (non-spatial and interspecific). However, support was found for an intraspecific latitudinal version of the rule where, in two thirds of species, male body size was found to vary more with latitude than female body size, with males having steeper body size-latitude relationships than females (Blanckenhorn *et al.*, 2006). Unfortunately, as the dataset was extremely large Blanckenhorn et al. (2006) do not divulge which species were in support of the adapted version of Rensch's rule.

Nonetheless, although based on m1L as a proxy for body size rather than real body size *per se*, male size was found to vary more with latitude than female size in the recent European *C. lupus* dataset, although regression slopes between latitude and proxy body size were shallower for males.

However, as discussed, the driving factors in latitudinal size variation, as well as sexual size dimorphism are complex, and hence the mechanisms behind the interplay of Rensch's rule and Bergmann size clines remains elusive, with further evaluation needed of how latitudinal body size trend relates to sexual size differences and their selective causes (Blanckenhorn *et al.*, 2006).

6.1.7. Bergmann's rule and Pleistocene Britain

In order to investigate whether Bergmann's rule was in operation during the Pleistocene in Britain, mean estimates of body mass for different age groups were compared, based on MIS 3 representing cool-temperate conditions, MIS 5a and 6 representing cold conditions and MIS 5e and 7 warm conditions. If Pleistocene *C. lupus* responded to climate change according to Bergmann's rule, it would be anticipated that body masses would be larger during cold climates, and smaller during warm climates.

MIS 5a had the largest mean estimated body mass, and although errors within the predictive regression model based on using lower carnassial length may mean that the reconstructed MIS 5a body mass is an underestimation, it remains the largest out of all the studied Pleistocene age groups in Britain.

MIS 3 had the second largest body mass estimate, although falling within the upper ranges of estimates from MIS 5e, 6 and 7. MIS 5e and 7 both had similarly smaller estimated mean body masses in comparison to MIS 5a. This pattern tentatively upholds the validity of Bergmann's rule.

However, as MIS 6 *C. lupus* was estimated as having the smallest mean body mass, as well as being within confidence interval range of the warmer age groups, it does not fit this pattern. As discussed, the body mass estimates from MIS 6 are based on one site only: Clevedon Cave, thus any variation present during the 60Ka period of MIS 6 (c. 190-130 ka BP) is not accounted for by this estimate. Combined with this, climatic conditions during MIS 6 were likely not uniformly cold. Ultimately, the limited information on MIS 6 makes it impossible to quantify whether *C. lupus* body size was responding to cold climate conditions.

This is in marked contrast to MIS 5a (c. 80-70 ka BP), where a range of sites within the 10Ka time span contribute to the mean body mass estimate, combined with good evidence of obligate cold climate conditions from analysis of beetles and molluscs.

Thus, Pleistocene *C. lupus* from Britain tentatively displays a Bergmannian response to climatic conditions, as found in its recent counterpart. However, more data are needed to better establish this body size pattern, as low numbers of individuals are problematic for MIS 2, 5c, 5e and 6, which importantly cover the warm and fully interglacial conditions of MIS 5e, and the deteriorating conditions of MIS 2 that are the temporally closest group to modern *C. lupus*.

6.1.7.1. Banwell Bone Cave: a test case of Bergmann's rule and sexual size dimorphism in Pleistocene Britain

As discussed, a latitudinal size cline exists in modern European *C. lupus*, with high latitude wolves generally being larger than those from lower latitudes. Thus, modern wolves appear to have a Bergmannian response to changing latitude.

Pleistocene *C. lupus* from Banwell Bone Cave have the largest mean estimated body mass in all the Pleistocene Britain age groups analysed. As discussed in section 6.1.2.3.1.1, conditions of MIS 5a were severely cold, based on analysis of beetles estimating palaeotemperatures of 7 to 11°C in summer and -10 to -30°C in winter Britain at this time (Maddy *et al.*, 1998). These restricted conditions are therefore analogous to high latitude climates today. Thus, it is plausible that the wolves of Banwell Bone Cave are of larger size because of Bergmann's rule.

The presence of sexual dimorphism at Banwell Bone Cave was explored by comparing Banwell *C. lupus* with the modern European high latitude males and females. This comparison was considered suitable because both groups are similarly of large size and apparently respond to Bergmann's rule in a similar fashion.

The comparison resulted in the identification of two size groups at Banwell Bone Cave. These groups plotted separately with the males and females of recent wolves and were found to be significantly different by *t* tests ($p<0.05$). Thus, the discrete size groupings present at Banwell potentially reflect the presence of males and females, and indicate similar levels of sexual dimorphism to those observed in modern European wolves.

As the putative male and female size groups at Banwell could be statistically differentiated, further investigation was called for as to whether the two groups at Banwell were statistically similar to the corresponding male/female clusters in the modern European *C. lupus* dataset. Interestingly whilst Banwell 'females' were found to be statistically similar to modern females ($p>0.05$), the Banwell 'males' were found to be significantly different from modern males ($p<0.05$).

It is encouraging to note the similarity in the females, consequently increasing the likelihood that the smaller Banwell group are indeed female. However, the same cannot be said for the males. It is possible that this result is symptomatic of the greater variation found in modern wolves that is not fully explicable by latitudinal (hence climatic) differences alone. Thus, male variation in size is perhaps more influenced by factors affecting sexual size dimorphism such as sexual selection.

It is important to note that potential problems exist in finding 'males' and 'females' at Banwell Bone Cave. The identification of sexual size dimorphism at Banwell is based on differences in m1L, used as a proxy for body size, rather than actual body size. To more

effectively gauge differences between sexes, further diagnostic material should be included, although this in itself is inhibited by the incomplete nature of the fossil record.

There is also the possibility that the two groups may represent different chronological age groupings within the cave, and thus different climatic conditions. In light of this, the smaller group could be potentially representing an interstadial (a brief interlude of warmer climatic conditions) rather than sexual dimorphism. Indeed, on the individual scale there may also be large differences in chronological age. In addition, the low species diversity characterising MIS 5a and Banwell in particular, may have exerted dietary stress on these wolves in terms of resources being more limited in a harsh environment, which will be discussed in section 6.2. Equally, the unusual absence of *P. leo* and *C. crocuta* from Britain at this time may also have affecting body size, which will be discussed in section 6.3.

6.2. Reconstructing canid diet during the Early, Middle and Late Pleistocene

Palaeodiet was investigated in *C. lupus, C. mosbachensis, C. etruscus* and *C. arnensis* to establish whether any variation present could be linked to temporal, geographic or climatic/environmental factors. Tooth breakage and wear was also assessed, as diet is highly influential on both these aspects.

Differences in diet between species were also examined. Evidence from modern canids was included in the analysis to examine whether any equivalence in diet was apparent with Pleistocene species, thereby allowing for inferences to be made on the palaeoecology of extinct taxa.

Variation was explored in the entire Pleistocene canid dataset using a PCA. Four principal components (PC) explaining the variation were extracted, with components 1 and 2 explaining the highest amount of variation. As the coefficients from PC1 were all positive, it is likely that this component summarises the within-sample size variation between the four canids. In light of this, PC2 likely represents the remaining variation that could not be explained by the size relationships (Clutton-Brock *et al.,* 1994).

Based on this relationship, the measurements highly correlated with PC1 (p1m3L, M1M2L, M2W, P4W, p2m3L and P3L) all indicated size, whilst the measurements correlated with PC 2 (M1W, p3p4B, p2p4L and M1L) all indicated differences in diet. Thus for the four main canids, the upper molars, jaw breadth at p3-p4 and premolar length (minus p1) are important palaeodietary indicators.

However, due to problems with linearity and complexity in the PCA, m1L, m1W, m1Ltrig, m1Ltal, m2L, m2W, p1p4L, m1m2D, m1m2B and P4L were all removed from the analysis. This removal rendered a large proportion of the variation in the dataset unexplored and unaccounted for. As the PCA was simply used as an exploratory method, and especially since it was not possible for all measurements to be included, all measurements were further investigated for temporal, regional and species differences.

6.2.1. Temporal differences in palaeodiet: palaeoclimatic and palaeoenvironmental implications

The presence of temporal variation in the palaeodiet of the Pleistocene canids will be discussed in the following sections, including its relationship to palaeoclimatic and palaeoenvironmental change, as well as palaeogeography.

6.2.1.1. Palaeodiet of *Canis etruscus* and *Canis arnensis*

The temporal palaeodietary analysis of *C. etruscus* comprised solely individuals from Val di Magra (Olivola F.U.) and sites of the Upper Valdarno Basin (Tasso F.U.). As mentioned in section 6.1, both sites are relatively close in age (Late Villafranchian, approximately 1.9 Ma and 1.8 Ma respectively), and *t* tests were used to examine whether any temporal differences were present between them. No significant differences were found, indicating that both age groups of *C. etruscus* were similar.

The number of broken and worn teeth was investigated in *C. etruscus*, with higher numbers of broken teeth found at Olivola (12.8%), in comparison to the Upper Valdarno (5.5%). As well as being correlated to increased individual age (Van Valkenburgh, 1988b), tooth breakage is also highly influenced by diet, particularly the amount of tough foodstuffs (Binder *et al*., 2002). However, the frequency of this breakage was found to be non-significant by Fisher's Exact test (used due to low expected counts in the analysis). Thus, the number of broken teeth here likely represents the ontogenetic age of the individuals rather than reflecting a change in palaeodiet through incorporation of tough foodstuffs. As no temporal differences were found between these sites, the absence of evidence for significant levels of breakage is consistent with this view.

In terms of tooth wear, which, like tooth breakage, is correlated to both individual age as well as the amount of tough foodstuffs in diet (Binder *et al*., 2002), *C. etruscus* from both Olivola and the Upper Valdarno displayed similar percentages of heavily worn teeth (18.0% and 20.6% respectively), with a higher percentage of slightly worn teeth at Upper Valdarno (39.7%). Olivola contained the highest amount of moderately worn teeth (56.4%). However, Pearson Chi-square tests found the tooth wear frequencies to be non-significant. As with the tooth breakage data, the distribution of tooth wear between the sites likely reflects ontogenetic age of individuals rather than differences in palaeodiet. Again, this fits well with the lack of temporal variation found between these sites.

Since the only available individuals of *C. arnensis* came from the Upper Valdarno, it was not possible to assess temporal variation in diet in this species. However, in terms of numbers of broken teeth, it was apparent that *C. arnensis* had very low percentages (1.2%), much lower than the sympatric *C. etruscus*. *C. arnensis* was also characterised as having a higher

percentage of slightly worn teeth (55.6%) in comparison to *C. etruscus*, with a lower percentage of moderate wear (35.8%) and heavy wear (8.6%).

Due to low numbers of broken and worn teeth, further tests on the significance of the frequency of breakage and wear were not possible, and hence it is difficult to make any firm inferences as to whether these differences reflect different ontogenetic ages of individuals or genuine differences in diet between species. However, when compared to sympatric *C. etruscus,* the evidence suggests that *C. arnensis* may have consumed less tough foodstuffs, and in particular had less tooth-bone contact, which would decrease the chances of tooth breakage. Less tooth-bone contact may indicate less gnawing of bone occurred and hence carcasses were either not fully utilised, or that scavenging was rare. By the same token, the lower levels of heavy wear also hint at a predominance of softer foods in the diet of *C. arnensis* in comparison to *C. etruscus*.

Thus, comparably higher levels of tooth breakage and wear in *C. etruscus* than in *C. arnensis* in the Upper Valdarno perhaps differentiate the canids on their food utilisation. Although frequencies of tooth breakage and wear for *C. etruscus* between Olivola and Upper Valdarno indicated differences may relate more to ontogenetic age than palaeodietary differences, in terms of species differences, the relatively higher percentages of heavily worn and broken teeth may suggest that *C. etruscus* incorporated tougher foodstuffs into its diet than *C. arnensis*, perhaps through fuller consumption of carcasses or scavenging.

6.2.1.2. Palaeodiet of *Canis mosbachensis*

Temporal variation in palaeodiet was also explored in *C. mosbachensis*. In Britain, the combination of low numbers of individuals and limited availability of assemblages proved problematic for analyses of late Middle Pleistocene sites containing *C. mosbachensis*. Therefore, as *C. mosbachensis* remains were most numerous from early Middle Pleistocene sites in Britain, in particular sites of MIS 13 age, the focus was on this period.

Early Middle Pleistocene sites were accordingly split, with the younger sites of Boxgrove and Sidestrand within MIS 13 grouped together and the reportedly older site of Westbury-sub-Mendip separated off, to allow for any temporal differences between them to be detected.

West Runton (correlated to MIS 17) yielded two individuals, represented by two m2 only. Thus, analysis of this site using one-way ANOVA was only possible for m2L and m2W, both of which were found to be significant. Subsequent *post hoc* tests for both m2L and m2W revealed that differences existed between Westbury and West Runton, yet both of these sites were found as similar to the Boxgrove-Sidestrand group.

Although only based on one tooth-type (m2), the relationship between Westbury and West Runton is of note, considering that one-way ANOVA found West Runton as similar to the Boxgrove-Sidestrand group. This potentially suggests some differences in molar crushing between these age groups, although further interpretation of other dental characters involved in the molar crushing complex, such as m1 talonid and upper molars, was not possible due to lack of West Runton material.

Examination of temporal variation in *C. mosbachensis* between the reportedly older Westbury and younger Boxgrove and Sidestrand used *t* tests for the remaining measurements. However, all measurements were found to be similar between these sites, as was the case with analysis of the m2 dimensions.

The inferred similarities in palaeodiet throughout MIS 13, combined with the difference found in m2 between Westbury and West Runton, are even more striking. Mean m2L and m2W were larger at Westbury (10.21mm, 7.66mm) than at West Runton (8.39mm, 6.28mm), indicating potentially increased molar crushing ability in the former. Although based on very limited information, it is possible that Westbury *C. mosbachensis* was able to incorporate more non-flesh foods into its diet, and thus had more dietary flexibility. An increase in dietary flexibility would enable *C. mosbachensis* at Westbury to supplement its diet with other foodstuffs such as vegetable and fruit material. The differences in m2 found between West Runton and Westbury may relate to the short-term climatic episodes represented in the Westbury assemblage; that due to the interceding cool period, *C. mosbachensis* adapted its molar crushing abilities to compensate. However, as no differences were found between older Untermassfeld, and younger Boxgrove and Sidestrand for this tooth or any of the other cranio-dental characters, it seems that perhaps other factors are involved, such as differences in carnivore competition and prey abundances. Since a larger canid, the extinct hunting dog-like *Canis* (*Xenocyon*) *lycaonoides*, was also present at Westbury, this difference may relate to competition between these canids, which will be further discussed in section 6.3.

Low numbers of individuals and sites were also problematic for the study of *C. mosbachensis* from mainland Europe. Very few individuals were recorded from sites of early Middle Pleistocene (age group 3.8, broadly equivalent to MIS 19-12) making further analysis impossible. Individuals from the Middle Pleistocene (European age group 3.4, broadly equivalent to MIS 12-9) however were slightly more numerous. For mainland European *C. mosbachensis*, individuals were most numerous from late Early Pleistocene (age group 4) site of Untermassfeld, correlated to slightly older than 1 Ma (Kahlke *et al*., 2011).

Temporal variation was examined by *t* tests between sites of mid Middle Pleistocene age (age group 3.4) and those of late Early Pleistocene (age group 4). However, all possible measurements were found to be non-significant, indicating no temporal differences between these age groups.

These age groups cover a much broader time span than of the chronologically better-constrained early Middle Pleistocene sites in Britain but perhaps, as a result, provide a clear indication of constancy in the diet of *C. mosbachensis* over time. As a final examination, sites correlated to the British Cromerian Complex (0.8-0.5 Ma, incorporating sites of MIS 13, as well as MIS 17 age) were compared to late Early Pleistocene site of Untermassfeld.

It was hypothesised that the differences found between Westbury and West Runton in the m2, might also be present in the late Early Pleistocene members. In addition, the amalgamation of British sites with *C. mosbachensis* into a larger group provides a more statistically reliable comparison with Untermassfeld, as well as permitting evaluation of change over a longer time frame. However, all measurements were found to be non-significant and no temporal variation in diet was accordingly found between any age groups of *C. mosbachensis*.

The overall lack of variation in *C. mosbachensis* from both mainland Europe and Britain suggests that *C. mosbachensis* was stable in its dietary behaviour. The difference found in m2 between Westbury and West Runton was not replicated in the continental sample, and without further material, this interesting relationship cannot be further explored. The lack of temporal variation in palaeodiet may relate to climatic conditions, which will be discussed in the following section.

Tooth breakage and wear were also examined for *C. mosbachensis* from Britain and mainland Europe. Low numbers of teeth were classed as broken for *C. mosbachensis* from

Britain, with Westbury containing the highest percentage (4.7%). In comparison, higher levels of tooth breakage were found in mainland European samples, with the late Early Pleistocene (age group 4, equivalent 1.38 - 0.78 Ma [MIS 19]) containing 5.0%, and notably the mid Middle Pleistocene (age group 3.4, equivalent MIS 12-9) containing 11.8% broken teeth.

Since only one site in Britain contained broken teeth, the frequency of breakage was only analysed for these mainland European age groups. However, the Chi-square test using Fisher's Exact test found the frequency of breakage to be non-significant between these age groups. Thus, it is inferred that tooth breakage here was more related to ontogenetic age rather than to differences in diet, which correlates well with the lack of temporal variation in diet between these groups.

Low levels of tooth wear were also present for *C. mosbachensis* from Britain. In particular, no heavy tooth wear was recorded from sites older than MIS 13, and only low levels of heavy wear (7.8%) were identified in the MIS 13 group itself.

As with the analysis of measurements, sites of inferred MIS 13 age were split in two, to allow for temporal comparison between the older Westbury group and the younger Boxgrove and Sidestrand group. However, the Pearson Chi-Square test found no significant differences in tooth wear frequency between these groups, which again correlates well with the lack of temporal variation in diet, as well as low tooth breakage.

For *C. mosbachensis* from mainland Europe, the late Early Pleistocene age group (age group 4) contained higher percentages of moderately worn teeth (43.8%) than both slightly worn (26.5%) and heavily worn (29.8%) categories. A similar pattern of wear was also present for the mid Middle Pleistocene age group (age group 3.4, equivalent MIS 12-9), with moderate tooth wear accounting for the highest percentages (52.9%). This similarity in the percentages of tooth wear correlates well with the temporal stability found in palaeodiet between these age groups, potentially indicating an extended period of dietary stability in *C. mosbachensis* on the continent perhaps reflecting temperate climatic conditions and similar regional conditions (see 6.1).

However, due only having one site (Voigtstedt) with limited canid material representing the early Middle Pleistocene in Europe (age group 3.8, equivalent MIS 19-13), any potentially variation during this period is lost. Also, in terms of tooth breakage and wear, only 17 teeth in total represent the mid Middle Pleistocene (age group 3.4), and thus provides a less

statistically reliable account of tooth wear frequency for this time. As previously mentioned, a similar situation was present for the early Middle Pleistocene group (age group 3.8), whereby only two teeth were accounted for at Voigtstedt providing extremely limited information on the frequency of tooth wear for this age group.

Due to low numbers of specimens, comparison of temporal changes in tooth wear frequency was only possible between the late Early Pleistocene Untermassfeld with the MIS 13 group from Britain. The Pearson Chi-square test found significant differences in tooth wear frequencies between these groups, indicating that something other than ontogenetic age was influencing tooth wear.

However, this result is in contradiction to the measurement data, which indicated temporal similarity in diet. Thus, the difference in tooth wear frequency here must relate to a factor other than diet. As discussed earlier, dietary stability in *C. mosbachensis* was related to overall warm interglacial conditions between the sites analysed of late Early and early Middle Pleistocene. Differences in tooth wear relating to climate are therefore difficult to fathom, and seem more likely related to carnivore competition and prey abundances, which will be discussed further in section 6.3.

Comparison between the British early Middle Pleistocene and late Middle Pleistocene was not possible due to low numbers of individuals and few sites (at present, only limited material is present at Cudmore Grove and Grays Thurrock, both of MIS 9). Further comparison would be of interest (if new material became available), to examine whether differences existed between the diets of British *C. mosbachensis* pre- and post- the Anglian glaciations in Britain.

Considering the extended period this stability spans (1 – 0.34 Ma) and the increasingly strong cycles in climate occurring post c. 1.2 Ma, it seems factors other than climate may have been influencing its stability, such as unimpeded migration onto the continent (allowing tracking of preferred prey), as well as carnivore competition and prey abundances, which will be discussed in section 6.3. The differences in tooth wear frequency between Untermassfeld, Westbury and Boxgrove were also of interest, especially since generally no differences in palaeodiet were found. Thus, this difference apparently relates to factors other than ontogenetic age and diet, and may also relate to differences in the carnivore community and prey abundance (discussed in 6.3.).

6.2.1.3. Palaeodiet of *Canis lupus*

Temporal variation in palaeodiet was also investigated in Pleistocene *C. lupus* from Britain and the European mainland, as well as compared to modern *C. lupus* from Sweden.

Variation in palaeodiet was examined between MIS 3, 5a and 7 in Britain using one-way ANOVA. In contrast to *C. etruscus* and *C. mosbachensis*, significant differences were found between these age groups in p4L, p4W, m1Ltrig, m1W, p3p4D, p3p4B, m1m2D, m1m2B, thus indicating variation through time.

Subsequent *post hoc* tests used for multiple comparisons between these age groups revealed that wolves from sites of MIS 3 and 5a age were significantly different from each other in terms of flesh-slicing ability and carnassial strength, as well as in p4L and jaw strength, which was focussed on jaw breadth at the premolars (p4L, m1Ltrig, m1W and p3p4B). The combination of significant differences in p4L and p3p4B potentially indicates concomitant changes relating to bone use, based on the strengthening of this part of the jaw linked to increased use of the p4 in bone cracking.

Individuals from MIS 5a and 7 were also significantly different from each other, both in jaw strength and in p4W (p4W, p3p4B, m1m2D, m1m2B). This is further suggestive of a relationship between p4 and changes in jaw breadth at the premolars. Combined with the differences in jaw depth and breadth at the molars, overall differences in jaw strength are indicative of potential differences in prey size, based on increased jaw strength relating to large prey capture.

In contrast, MIS 3 and 7 *C. lupus* were found to be similar across all measurements. This indicates that the MIS 5a group is responsible for the majority of variation between the various age groups. In terms of similarity, MIS 3 and 5a wolves were similar in p4W and jaw breadth at the premolars and depth at the molars (p4W, p3p4B, m1m2D), whereas MIS 5a and 7 assemblages were similar only in p4L.

As temporal variation in palaeodiet was found between assemblages of MIS 3, 5a and 7 age, the modern *C. lupus* group from Sweden was then included in the analysis to assess whether inferred differences in diet could be extended into the Holocene. A modern assemblage from Sweden was used exclusively as it represents a relatively localised population of wolves with known ecological parameters and climatic conditions. Thus, it was anticipated that any differences detected would not be masked by regional differences within the modern sample.

As well as the analysis of MIS 3, 5a and 7, one-way ANOVA found further measurements to be significant between all age groups, including p4L, p4W, m1Ltrig, m1Ltal, m1W, m2L, m2W, p3p4D, p3p4B, m1m2D, m1m2B, P4W, M1L, M1W, M2W and M1M2L.

The subsequent *post hoc* tests revealed that modern *C. lupus* was significantly different from all other age groups. Between MIS 3 and the present day, differences developed in p4 length, lower molar grinding capacity, M1L, and jaw strength at the molars (p4L, m1Ltal, m2W, m1m2D, M1L). These changes relate mainly to the molar crushing complex, suggesting differences in the ability to crush non-flesh foods. The significance of the difference in p4 length is, however, less clear, since no change was observed in either m1Ltrig or m1W, or in p3p4B or p3p4D.

Differences between modern and MIS 5a *C. lupus* related to p4 shape, meat slicing ability, carnassial strength, jaw strength at the molars as well as upper molar complex (p4L, p4W, m1Ltrig, m1W, m1m2D, P4W, M1L, M1W, M2W). This suggests that more differences existed between MIS 5a and modern wolves in the ability to utilise bone, slice flesh, and crush other non-flesh foods, as well as in jaw strength, than between MIS 3 and modern wolves.

Although changes in p4 have been linked to increased bone utilisation, especially when combined with differences in jaw strength at the premolars, it is also possible that changes in m1 and P4 influence p4 shape, based on their occluding positions in the dental complex. To determine which is having the greater effect, other factors affecting diet need to be explored, such as climate and prey availability, both of which will be discussed in the following sections.

Differences between modern and MIS 7 *C. lupus* related to carnassial strength, jaw strength and the molar crushing complex (m1W, m2L, p3p4D, p3p4B, m1m2B, M1L, M1W, M2W). Thus, differences in jaw strength may reflect variation in the size of prey taken between MIS 7 and modern wolves, whereas the differences in molar crushing capacity suggest variation in the incorporation of non-flesh foods into the diet between modern *C. lupus* and those of MIS 7.

Between all age groups, jaw strength at the molars and the buccal length of the M1 (m1m2D, M1L) were consistently different between recent *C. lupus* and Pleistocene *C. lupus*, suggesting the importance of these attributes in recent wolves compared to its

earlier conspecifics. Hence, modern wolves require deeper jaws at the molars, and a longer buccal edge of the M1 in comparison to the Pleistocene wolves.

It is interesting to note that differences in p4W and meat slicing ability were consistently related to recent *C. lupus* and MIS 5a, whereas differences in lower molar crushing ability were consistently related to recent *C. lupus* and MIS 3, as well as molar crushing combined with jaw strength were specifically related to recent *C. lupus* and MIS 7. Thus, clear dietary separation between these age groups is suggested. To further elucidate how these differences separated the age groups, a stepwise DFA was carried out, which elucidated the proportion to which each significant measure varied between each age group. The results from the stepwise DFA will be discussed later.

Temporal differences in diet were also assessed in Pleistocene *C. lupus* from mainland Europe. As many sites were less well chronologically-constrained than in Britain, much of the European material had to be amalgamated into broad age groups in order to allow comparison across time and space. The amount of well-dated material was therefore limited, thereby reducing numbers of individuals and available measurements for analysis.

As a result, only m1Ltrig, m1Ltal and m1W were analysed by one-way ANOVA between age groups representing the late Middle to mid Late Pleistocene *C. lupus*. These measurements were all found to be non-significant, implying that there were no temporal differences in the m1 measurements.

When the mainland European age groups were compared to modern *C. lupus* from Sweden however, significant differences were found in p4L, m1Ltrig, m1Ltal, m1W, M1M2L. The subsequent *post hoc* tests indicated that modern *C. lupus* was significantly different from the late Middle Pleistocene age group (age group 3, equivalent MIS 7-6) in meat slicing ability and lower carnassial strength (m1Ltrig and m1W), as well as in the buccal length of the upper molar complex (M1M2L).

Likewise, differences in upper molar grinding length (M1M2L) were also found in modern *C. lupus* when compared to the mid Late Pleistocene group (group 2.4, equivalent MIS 3), as well as differences in m1m2D, based on the results of *t* tests. Interestingly, all measurements were similar between the early Late Pleistocene age group (group 2.8, equivalent MIS 5e-a) and modern *C. lupus*. As this age group was broadly correlated with MIS 5, this contrasts markedly with British material of MIS 5a age, whereby multiple

differences in bone eating behaviour, flesh slicing, molar crushing and jaw strength were indicated in comparison to modern wolves.

Although based on fewer individuals and sites, the differences in the dietary measurements between all analysed Pleistocene *C. lupus* from the European mainland and recent *C. lupus* were overall related to molar crushing ability, indicating a general difference in the ability to incorporate non-flesh foods between European Pleistocene and modern *C. lupus*.

Nonetheless, differences in the m1 trigonid length and width were unique to the late middle Pleistocene age group 3. Interestingly these differences with modern wolves were not replicated in the analysis with the broadly equivalent MIS 7 British age group, which indicated differences relating to molar crushing and jaw strength in comparison to modern wolves. Similarly, the differences in jaw strength between modern *C. lupus* and the mid Late Pleistocene age group 2.4 were not seen in the equivalent British age group (MIS 3), which were more related to molar crushing, rather than jaw strength. These regional differences will be further discussed in section 6.2.2. To further elucidate the proportion to which each significant measure varied between each age group, DFA was carried out.

As the diet of Pleistocene *C. lupus* was demonstrated as varying through time, differences in the frequency of tooth breakage and wear were also explored. In Britain, wolves from MIS 5a sites contained the highest percentage of broken teeth (8.0%) in comparison to those from MIS 3 (2.5%) and MIS 7 (2.6%). The frequency of breakage was found to be significant between MIS 3 and 5a, based on Pearson Chi-square tests and therefore interpreted as reflecting differences in palaeodiet between the two groups. However, tooth breakage frequencies for both MIS 3 and 7 groups and MIS 5a and 7 groups were found to be non-significant using Fisher's Exact test. The non-significant outcome indicates that the frequency of breakage between these different groups of wolves was not unusual, and is therefore likely an indication of ontogenetic age.

The non-significance of the result between MIS 5a and 7 was not expected, based on the significant result found between MIS 3 and 5a, and the higher percentage of broken teeth identified from MIS 5a. It is possible that lower numbers of total teeth for MIS 7 (n=76) in comparison to MIS 5a (n=187) and MIS 3 (n=161) are having an effect on the analysis.

Due to low numbers of specimens, statistical analysis of tooth breakage was not possible for mainland European *C. lupus*. Although the late Late Pleistocene age group (group 2, equivalent MIS 2) had the highest percentage of broken teeth (33.3%), this result was

based only on two teeth. The early Late Pleistocene age group (group 2.8, equivalent MIS 5e-a) had a much more robust estimate of broken teeth (2.2%), since the counts were based on a total of 46 teeth. When compared with British material of similar age, this low percentage of breakage is notable, since the British MIS 5e sample had 4.1% broken teeth (based on a total of n=49 teeth), the British MIS 5c group had 22.2% broken (total teeth n=9), and the British MIS 5a sample had 8.02% broken teeth (total teeth n=187).

From the analysis of tooth wear, MIS 5a *Canis lupus* showed the highest percentage of severely worn teeth (48.7%), MIS 3 had the highest percentage of moderately worn teeth (49.7%), whilst MIS 7 had the highest percentage of only slightly worn teeth (46.1%). The level of severe tooth wear seen in the MIS 5a group correlates well with the high numbers of broken teeth previously observed. However, both MIS 3 and 7 had similarly low levels of broken teeth, suggesting that in these age groups, tooth wear was more important than tooth breakage.

The frequency of tooth wear between MIS 3 and 5a wolves, MIS 3 and 7 wolves, and finally MIS 5a and 7 wolves was to be significant for all groups by Pearson Chi-square tests. This indicates that between all age groups, the frequency of wear was unusual, and therefore not related to ontogenetic age. This correlates closely with the palaeodietary variation found in *C. lupus* and acts as a clearer indicator than levels of tooth breakage.

For mainland European *C. lupus*, based on percentages of worn teeth by age group, the mid Late Pleistocene (age group 2.4) contained the highest percentages of heavily worn teeth (60.0%), with the late Middle Pleistocene group (age group 3) containing the most moderately worn teeth (81.8%). The early Late Pleistocene group (age group 2.8) contained the most slightly worn teeth (21.7%). However, due to low numbers of teeth, only the mid Late and early Late Pleistocene age groups (age groups 2.4 and 2.8) were analysed further, although a Pearson Chi-square test found the frequency of tooth wear between these groups to be non-significant.

The analysis of tooth breakage and wear for mainland European *C. lupus* was therefore not as revealing as for its British counterparts, likely due to the lack of well-dated material. It seems that tooth wear in particular correlates well with the temporal variation in diet found between MIS 3 and 7, and in particular for MIS 5a.

To further explore the temporal differences in diet, a stepwise DFA was used. Based on the best predictors of group membership being selected by the Discriminant Function Analysis, differences in diet of each age group were revealed by the measurements correlated to the discriminating functions created by the model.

As temporal variation in diet was only found in *C. lupus*, only this species was included in the Discriminant Function Analysis. Furthermore, only British material from MIS 3, 5a and 7 was used, in combination with recent *C. lupus* from Sweden, since these were the only groups with high numbers of individuals.

The stepwise discriminant model was created in 11 steps, which selected M1M2L, p4L, M1W, m1m2D, m1m2B, P4W, p1m3L, p3p4D, p3p4B, p1p4L and m1L as the best predictors of age group membership. Three discriminant functions were created, explaining 100% of the variance, with the first two functions explaining the highest proportion (91.7%). These form the focus for the results presented below.

Chi-square tests found the functions significant (p<0.05), with high discriminatory ability. Based on the aforementioned three discriminant functions, the stepwise DFA correctly classified 95.1% of original cases, and 91.3% using cross-validation. Based on the cross-validated model, the stepwise selected measurements correctly classified 93% of modern specimens, 80% of material of MIS 3 age, 96.7% material of MIS 5a age and 90% of material of MIS 7 age.

Function 1 explained the highest proportion of variation (53.6%) and separated modern specimens as well as those of MIS, 3 and 7 age from MIS 5a, highlighting that the MIS 5a wolves were characterised by longer p4L and broader m1m2B, with narrower M1W and P4W (p4L, M1W, m1m2B and P4W) based on their positive and negative coefficient scores.

Function 2 explained less of the variation (38.1%) and separated modern specimens, as well as those of MIS 3 and 7 age the most, with MIS 5a relatively less separated and plotting between these age groups. This indicates that the modern *C. lupus* sample possessed a longer length of the upper molar grinding complex, in addition to increased jaw strength at the premolars and molars (M1M2L, m1m2D and p3p4B).

Based on the separation of the MIS 5a group by function 1, it is suggested that increased breadth of the jaw at the molars relates to improved jaw strength. This implies that the MIS 5a *C. lupus* had a greater ability to hunt large prey, beyond that seen in the other age groups. Although the separation between the modern and MIS 3 and 7 wolves was less

marked than for the MIS 5a group, the former possessed comparatively weaker jaws and are therefore considered to have been somewhat less able to obtain large prey. MIS 7 *C. lupus* in particular had the narrowest jaws related to this function, and would therefore have been the least able to hunt and capture large prey.

These observations are particularly interesting for both MIS 3 and 7 *C. lupus*, since both periods were characterised by the presence of a diverse large herbivore guild. The implications will be discussed further in section 6.3.

Modern *C. lupus* and those from MIS 3 and 7 were all differentiated from the MIS 5a animals by having a wider M1, and were thus better equipped for crushing non-flesh foods. It is consequently inferred that a higher proportion of non-flesh foods were incorporated into their diets during these periods. In contrast, MIS 5a *C. lupus* possessed a much narrower M1, with the reduction in the molar crushing complex implying that meat was a more important component of wolf diet at this time.

Function 1 also separated the age groups by flesh slicing ability based on P4L. MIS 5a wolves were found to have a higher flesh slicing ability based on the presence of a narrower P4. In combination with the reduced molar crushing capacity, this suggests that MIS 5a *C. lupus* was more adapted to hypercarnivory during the Early Devensian than at any other time.

Whilst wolves of other ages were all obviously carnivorous, their reduced ability to slice flesh quickly, combined with increased molar crushing ability, indicates that higher proportions of other, non-flesh foods were also incorporated into their diets, in comparison to the Early Devensian group. Thus, modern *C. lupus* and those from the Middle Devensian (MIS 3) and penultimate interglacial (MIS 7) apparently incorporated a wider variety of food into their diets, thereby demonstrating more flexibility in this aspect of their behaviour.

The separation of MIS 5a *C. lupus* on p4 elongation is interesting. Based on the high levels of tooth breakage and wear present in the MIS 5a group indicating that harder foods were incorporated into the diet at this time, it seems likely that the p4 is responding to increased usage related to higher bone consumption. This also correlates well with the observed reduction in molar crushing in the MIS 5a group – if *C. lupus* was less able to crush bone using its molars, the p4 may have developed greater importance as a bone cracking device. This will be further discussed in the following section. Wolves from other age groups all had

shorter p4 lengths, which if related to bone use, correlates well with lower levels of tooth breakage and wear seen in the MIS 3 and 7 samples.

Function 2 separated modern *C. lupus* from the other age groups by having increased length of the buccal upper molar complex and increased jaw strength at the premolars and molars. The longer upper molar length correlates well with function 1, indicating the overall increased molar crushing ability of modern *C. lupus* in particular, in comparison to all other groups. MIS 3 and 7 wolves were most clearly differentiated from modern *C. lupus* on this function, with MIS 5a situated in between the two clusters. Thus, although function 1 revealed that both MIS 3 and 7 wolves have wider M1 than in the MIS 5a group, they conversely have shorter buccal lengths in the upper molar complex. This is suggestive of an anterio-posterior shortening in relation to M1 width.

The intermediate position of the MIS 5a group in terms of buccal molar length is also interesting, since although they have narrower upper molars, the buccal edge is relatively longer than witnessed in the MIS 3 and 7 groups, which display greater molar crushing capabilities. Thus the purpose of the buccal edge must be more complex than simply part of the larger crushing apparatus. Its direct occlusion with the m1 talonid and m2 may be responsible for this length variation, although these measurements were not highly correlated with either function.

As previously mentioned, modern *C. lupus* is distinctive in having deeper and therefore stronger jaws than both MIS 3 and 7 *C. lupus*, with MIS 5a situated in between. This may appear somewhat unusual, as function 1 separated the age groups based on broadness of the jaws at the molars. Thus, MIS 5a *C. lupus* was found to have broad but shallow jaws at the molars, whereas modern *C. lupus* had deep but narrow jaws at the molars. Both MIS 3 and 7 wolves shared shallower and narrower jaws by comparison.

Broadness and depth of jaws have both been related to jaw strength and the ability to apprehend large prey by resisting heavy loading and strain. However, the separation of depth and breadth in the age groups may highlight another purpose. As jaw breadth clearly separated the MIS 5a group, this character may be more related to increased bone use, as earlier considered with the combined significance of p4 and p3p4B in ANOVA for MIS 5a wolves.

With the functions combined, the stepwise DFA indicated the importance of p4L, M1W, m1m2B, P4W, M1M2L m1m2D and p3p4B in separating the different age groups. The

estimation of mean body mass (section 6.1) of *C. lupus* across these age groups indicated that modern and MIS 5a wolves were most similar in size, and slightly larger than *C. lupus* from MIS 3 and 7, although all were within the body mass variation of the species as a whole. The minor variations in body mass noted are accordingly thought to have minimal influence on the range of measurements, thereby allowing genuine palaeodietary differences between groups to be revealed.

Despite the fact that they represent different palaeoclimatic episodes, late MIS 7 *C. lupus* was found to be similar to MIS 3 by ANOVA, and from the DFA both were found to have increased molar crushing ability, reduced flesh slicing ability, as well as shallower and narrower jaws than both recent and MIS 5a *C. lupus*. Hence, wolves from MIS 3 and 7 incorporated larger amounts of non-flesh foods into their diet, were less able to slice flesh quickly, and had weaker jaws and thus were less able to easily manipulate the largest of prey in comparison to MIS 5a wolves.

This interesting parallel suggests that palaeoclimatic factors alone may not explain the similarity. As discussed, temperate conditions similar to today were present during late MIS 7, whereas mean summer and winter temperatures were much colder than present during MIS 3. However, the key point of comparison is that both periods are characterised by relatively treeless, open grassland environments, with moderately high species diversity and including an abundance of large prey and also similar small mammal prey including *M. oeconomus* and ground squirrels (*Citellus citellus* during MIS 7, *Spermophilus major* during MIS 3).

There were, however, significant differences in tooth wear between the two groups with MIS 7 wolves having a higher percentage of slightly worn teeth and MIS 3 wolves having more moderately worn teeth. As environmental openness and prey diversity were similar during both periods, it is possible that increased levels of grit and dust were responsible for the differences observed, in terms of causing increased tooth wear. Because of lowered sea level exposing continental shelves and a reduction in surface vegetation, atmospheric dust loads were higher during the cold periods of the Quaternary, in comparison to warm periods (Lambert *et al.,* 2008). Increased levels of airborne dust in MIS 3, the middle part of the last cold stage, may therefore have been incidentally ingested by wolves during respiration, feeding (on plant or animal sources) or grooming, with consequent effects on tooth wear.

In contrast, modern *C. lupus* from Sweden was found to be significantly different from both MIS 3 and 7 wolves in terms of its increased crushing and flesh slicing abilities and stronger jaws. These differences are interesting as the modern sample comes from a temperate period, the late Holocene, and should therefore be comparable with MIS 7 (an interglacial) and to a certain extent with MIS 3, the warmest part of the last cold stage. The disparities reinforce the importance of openness of the environment. Central Sweden, from where the modern sample was sourced, is predominantly boreal forest comprised of pine and spruce, as well as birch and conifer (Arnborg, 1990), and 'closed' in comparison to the open environments that characterised MIS 3 and 7, and also MIS 5a.

The difference in vegetation cover may therefore be a factor in modern *C. lupus* having increased crushing ability, as well as deeper jaws. These modifications may relate to the pursuit of prey being more difficult in closed habitats, and with increased hiding places for small to medium prey making hunting a more labour-intensive exercise for less nutritional reward. In boreal forest across northern Europe, the majority of ungulates are of large body size (from c.200kg in adult red deer to c.800kg in elk; Nowak, 1991) and may be difficult to find in the forest, solitary or only seasonally available. Therefore, despite the difficulties and dangers in subduing such animals, opportunities to take such large prey must be seized, hence the requirement for much stronger jaws in comparison to MIS 3 and 7.

Significant differences were found between the MIS 5a sample and the other groups. These differences likely relate to the extreme cold conditions of the Early Devensian, as indicated by analysis of the beetle assemblage at Cassington, estimating mean summer temperatures of 7 to 11°C and winter temperatures of -10 to -30°C in Britain at this time (Maddy *et al*., 1998). Further examination using the DFA confirmed that MIS 5a *C. lupus* was more able to slice flesh quickly, less able to crush non-flesh foods, had an elongated p4 (potentially for bone utilisation), and broader rather than deeper jaws. The MIS 5a cold climate *C. lupus* was thus more adapted towards hypercarnivory and bone-eating than during any other climatic period studied, either Pleistocene or modern.

Low species diversity, and thus low prey diversity, was one of the key differences between MIS 5a and the other age groups considered, with the Banwell fauna in particular containing only *B. priscus*, *R. tarandus* and hare (*Lepus timidus*) as possible prey species. In studies of both *C. lupus* and *C. dirus* from the Late Pleistocene site of La Brea, limited food availability was regarded as the trigger for carcasses being consumed more fully (Binder *et*

al., 2002; Van Valkenburgh and Hertel, 1993). As a consequence of low resource availability, competition from other carnivores led to fuller as well as more rapid consumption of carcasses, as well as increasing food-related conflict and aggression (Van Valkenburgh and Hertel, 1993). The rapidity of consumption resulted in increased bone consumption, which was responsible for higher incidences of tooth wear and breakage (Binder *et al.,* 2002).

In light of this, and based on the presence of cold-climate conditions combined with low prey diversity and a lack of alternative plant foods (predominantly herbaceous Arctic steppe species identified at Cassington [Maddy *et al*., 1998]), it is inferred that MIS 5a *C. lupus* was under high levels of dietary stress. In a severely resource-limited environment such as that of the Early Devensian in Britain, *C. lupus* would need to fully consume carcasses, and hence increase bone consumption, giving rise to the high levels of tooth wear and breakage found. It is also likely that *C. lupus* may have scavenged carcasses, potentially either from other wolf packs, or from the very large brown bear that was the only other large carnivore present during MIS 5a in Britain. The theory that *C. lupus* may have adopted a scavenging and bone consuming behaviour is also supported by the absence of spotted hyaena (*Crocuta crocuta*) from Britain at this time (Turner, 1981, 2009). Although spotted hyaenas hunt, their absence would have allowed *C. lupus* to exploit fully the bone consumption niche.

The increased tooth wear and breakage seen in MIS 5a wolves may also indicate that scavenged carcasses were frozen at the time of consumption, although perhaps only seasonally. According to Haynes (1982), occasional scavenging on frozen carcasses by modern *C. lupus* does occur, although the preference is for fresh kills. It therefore seems probable that with lower resource availability, a heavier reliance on scavenging would be more commonplace, particularly during the seasonal migrations of the two large herbivores present at this time, *R. tarandus* and *B. priscus*. Frozen carcasses would therefore have represented a valuable resource at a time of nutritional stress. Increased hypercarnivory and reduction in the post-carnassial molars in MIS 5a *C. lupus* also correlates well with more rapid consumption of carcasses, notably an increased flesh slicing ability that would be advantageous in a resource limited, difficult environment.

Nevertheless, the incorporation of increased amounts of bone into the diet during MIS 5a may seem incongruous with the observed decrease in molar crushing ability. For canids, bone utilisation is generally accomplished by crushing by the molar complex (Werdelin,

1989). However, the reduced crushing ability of MIS 5a wolves implies that bone may have been manipulated by a different mechanism at this time. As mentioned earlier, the p4 in carnivores is thought to have a relationship with the amount of bone incorporated into diet (e.g. Van Valkenburgh, 1988a). Therefore the importance of an elongated p4 in MIS 5a wolves (as found in the DFA), and the differences in p4L and p4W found by ANOVA post hoc tests, suggests two possibilities: that elongation of p4 either facilitates hypercarnivorous adaptation in some way, based on occlusion with P4, or that it otherwise enables further bone consumption.

The reduction in molars potentially supports the latter hypothesis in wolves, since by not being able to crush bones effectively, the p4 might instead have served to crack bones quickly, in a manner akin to hyaenas. As outlined in Chapter 4, both spotted hyaenas and wild dogs have been known to utilise other non-specifically adapted teeth in bone cracking and crushing (Van Valkenburgh, 1996). Hence, it is therefore is possible that the p4 in MIS 5a *C. lupus* could have been utilised in similar fashion and that together with the reduction in molars, an elongated p4 might have conferred some sort of speed advantage, when rapid feeding would be advantageous.

As noted, palaeodietary variation in *C. lupus* may reflect adaptations to the increasingly dramatic climatic oscillations of the late Middle and Late Pleistocene. Consequently, to further examine whether dietary variation could be identified between wolves from cold and warm climate episodes, the well-dated British age groups were amalgamated into climate-type groupings. Thus a cold climate group was established for wolves from sites of MIS 3, 5a and 6 age, while a warm climate group contained wolves from sites of MIS 5e and 7 age.

Subsequent *t* tests found significant differences between the cold and warm groups, suggesting climate-driven differences in p4 shape, broadness of the jaw at the premolars and molars, and flesh slicing ability (p4L, p4W, m1Ltrig, m1W, p3p4D, p3p4B, m1m2D, m1m2B). Thus, these measurements were found as statistically larger in the cold group than in the warm group.

The percentages of tooth breakage and wear between members of the cold and warm climatic groupings also show variation perhaps related to climatic period; with MIS 5e and 7 containing fewer broken and less heavily worn teeth in comparison to MIS 5a in particular, which contained the highest number of broken and heavily worn teeth.

However, the measurements found to be significant in cold climates were similar to those specifically relating to MIS 5a. It is therefore worth noting that the significantly different measurements of MIS 5a may be driving the differences between the cold and warm climate groupings, and biasing these results. As discussed, MIS 5a was a period of extreme cold, yet other factors particular to this episode may have enhanced the level of difference observed, such as the unusually low species diversity of the period, combined with suggested re-isolation of Britain from mainland Europe at this time (Currant and Jacobi, 2011), which will be discussed later.

To conclude, clear temporal variation in diet exists in *C. lupus*. Differences between modern *C. lupus* and MIS 5a *C. lupus* were found to be particularly important, relating to differences in molar crushing ability, jaw strength, flesh slicing ability and bone use. The degree of tooth wear was also subject to temporal variation, revealing MIS 5a *C. lupus* to have the highest numbers of broken and most severely worn teeth. It was suggested previously that apparent palaeodietary stability in Early Pleistocene *C. etruscus* was related to minimal differences in climate between the Olivola and Tasso F.U.s. Similar stability in *C. mosbachensis* might relate to factors such as being able to freely migrate into Europe during the late Early and Early Middle Pleistocene, as well as perhaps similar levels of competition and stable prey abundances. In contrast, it seems likely that increasing palaeoclimatic instability after the "Mid-Pleistocene Revolution" (*c*. 1.2 million years ago) and the concomitant impacts on vegetation and prey availability (see 6.1) may have been responsible for much of the dietary variation in late Middle and Late Pleistocene *C. lupus* in particular, although factors such as openness of the environment, prey species diversity, presence of plant foods and availability of trophic niches were also important.

6.2.2. The effect of regional differences on diet

No regional comparisons were possible for either *C. etruscus* or *C. mosbachensis* due to lack of material and coeval sites. However, the overall lack of dietary variability in the two taxa suggests that regional differences may have been minimal at this time. Also, as discussed in section 6.1, Britain was a peninsula of the European mainland through much of the Early and Middle Pleistocene (Funnell, 1995) allowing ebb and flow of species across western and central Europe and reducing the effects of local populations.

In contrast, temporal variation in the palaeodiet of *C. lupus* appears to be much more strongly determined by palaeoclimatic drivers, and the subsequent relationship with environmental type and species diversity. As discussed in section 6.1, regional differences may be caused by biogeographical barriers such as mountains and glaciers, or (in the case of Britain) through island isolation caused by climate-driven eustatic changes. Both affect the movements of large migratory prey species, in particular, which would have been key prey for Pleistocene *C. lupus*.

The effect of regional differences was investigated between Britain and mainland Europe by comparing age-correlated groups. No regional differences in diet were found between the continental mid Late Pleistocene age group (group 2.4) and British MIS 3 using *t* tests. This is consistent with the fact that Britain was reconnected to mainland Europe during this time, allowing migration of species across the extensive open steppe environment of the southern North Sea basin, and promoting similarity in faunal assemblages.

For the few available measurements of m1 and M1, continental sites of the late Middle Pleistocene in Europe (age group 3) were compared with those of MIS 6 and late MIS 7 age in Britain. The mainland European sites of this age group included only Weimar-Ehringsdorf, Germany, correlated with MIS 7 (Schreve and Bridgland, 2002), and Dobelhaldeschacht, Germany, which was correlated to the late Middle Pleistocene (Ohmert, 1988) (m1 n=3, M1 n=2). British sites of late MIS 7 age including Bleadon Cave, Hutton Cave, Ilford and Marsworth, and Clevedon Cave for MIS 6 were compared (m1 n=13, M1 n=10). No significant differences were found by *t* tests, thus indicating no regional differences present in palaeodiet.

In contrast, *t* tests found significant differences between the continental early Late Pleistocene age group (group 2.8, equivalent MIS 5e-a) and the British sites covering MIS 5e-a, in p4W, m1Ltrig, m1W and M1W. The broad age group of the early Late Pleistocene in mainland Europe encompasses the distinct climatic oscillations of MIS 5, with MIS 5e representing temperatures significantly higher than today in Britain and MIS 5a in particular representing severely cold tundra conditions, as discussed in section 6.1. Conditions during MIS 6 were also very cold, based on evidence of glaciation in eastern Britain (Hamblin *et al*., 2005) and northwestern Europe (Busschers *et al*., 2008), whereas during MIS 5a no evidence of glaciation is present in Britain, just extreme cold. Thus, more extreme climatic differences during the early Late Pleistocene are not solely responsible for the regional differences found between Britain and Europe.

The majority of the mainland European material of the early Late Pleistocene age group (group 2.8) was from Bad Canstatt (Villa Seckendorf), Germany. Based on its correlation to the 'steppennagerschicht' (Rodent layer) present in the Untertürkheim travertines, situated opposite the site on the opposing bank of the River Neckar (Ziegler, 1996), Bad Canstatt (Villa Seckendorf) has been correlated to between MIS 5e-c in age (Wenzel, 1998). Further to this, the presence of cold adapted species such as *L. lemmus* and *D. torquatus* was considered by Ziegler (1996) as having more of an Early Weichselian affinity, also supported by the presence of *R. tarandus* and *M. primigenius*.

The lack of well constrained correlation of this site with other sites of the early Weichselian in Europe, makes reliable comparison with the British early Devensian difficult, particularly to the sites of the Bacon Hole MAZ of MIS 5c. Thus, it was not possible to establish whether regional variation or climatic variation was responsible for the significant differences between Britain and mainland Europe during this period.

Nonetheless, the consistently different MIS 5a record in Britain may be the source of the differences found here. As previously discussed in section 6.1, Britain was probably isolated for all of MIS 5. However, based on the very low diversity fauna present during MIS 5a, it was suggested that possible reconnection occurred during MIS 5b (Currant and Jacobi, 2001; Gilmour *et al*., 2007) introducing the large mammals into Britain prior to re-isolation during MIS 5a. Thus regional differences between Britain and mainland Europe may have existed, although difficult to compare due to lack of MIS 5a correlated sites in mainland Europe used in this research.

As discussed, the interplay of cold climatic conditions and low species diversity caused high levels of dietary stress for *C. lupus*, thus resulting in dietary modifications that allowed rapid full consumption of carcasses. Although Britain was isolated from the continent at this time, there is not enough evidence suggesting that isolation affected prey abundance. However, it would be expected that any period of isolation would potentially enhance differences between British and continental populations.

In summary, regional correlation exists between *C. lupus* from Britain and mainland Europe during the late Middle Pleistocene (MIS 6-7) and mid Late Pleistocene (MIS 3), although based on comparatively fewer mainland European sites and less material. Regional differences were only found during the early Late Pleistocene (MIS 5e-a), however lack of age-correlated sites to the distinct climatic episodes of this period (e.g. from MIS 5a) in Europe makes regional related differences difficult to discern.

6.2.3. Comparison of dietary differences between the Pleistocene canids

The dietary differences between the various Pleistocene canids were explored in order to compare their palaeoecology, as well as competitive interactions. All measurements were found to be significant by one-way ANOVA, and subsequent *post hoc* tests revealed that *C. lupus* was significantly different from *C. mosbachensis, C. etruscus* and *C. arnensis* in all measurements.

Although differences were present between the canids, they also often shared similarities. *C. mosbachensis* was significantly different from *C. etruscus* in p4 shape, premolar row length, length of cheek teeth and upper molars (p4L, p4W, m2L, p1p4L, p2p4L, p1m3L, p2m3L, M1L, M1W), but similar in upper and lower carnassial blade length and width, lower molar complex, jaw strength, upper premolar row length and aspects of the upper molars (m1Ltrig, m1Ltal, m1W, m2W, p3p4D, p3p4B, m1m2D, m1m2B, P3L, P4L, P4W, M2W, P1P4L, M1M2L).

When compared to *C. arnensis,* differences only in p4W, carnassial blade length and width (m1Ltrig, m1W and P4L) were present in *C. mosbachensis*, whilst similarities in p4L, lower molar complex, lower premolar and cheek tooth lengths, jaw strength, upper carnassial width, upper molar complex, length of upper premolars and all teeth (m1Ltal, m2L, m2W, p1p4L, p2p4L, p1m3L, p2m3L, p3p4D, p3p4B, m1m2D, m1m2B, P3L, P4W, M1L, M1W, M2W, P1P4L, P1M2L, C1M2L, M1M2L) dominated.

C. etruscus was significantly different from *C. arnensis* in most measurements, involving p4 shape, carnassial blade length and width, lower molar complex, length of premolars and cheek teeth, jaw strength and upper molar complex (p4L, p4W, m1Ltrig, m1Ltal, m1W, m2L, m2W, p1p4L, p2p4L, p1m3L, p2m3L, p3p4D, p3p4B, P3L, P4L, M1L, M1W, M1M2L). Similarities existed only in jaw strength at the molars, width of M2 and length of upper premolars.

These differences and similarities were further explored using stepwise DFA, to examine how the measurements could predict membership of each species. As well as revealing any dietary differences present, this technique will also permit unattributed or fragmentary material within existing museum collections, for example, to be more confidently allocated to a species. The stepwise discriminant model was created in 11 steps, which selected m1m2D, m1Ltrig, P4W, p4W, p1p4L, p4W, M1L, m1m2B, M1M2L, p3p4D, p2p4L and M2W as the best predictors of species group membership. Three discriminant functions were

created explaining 100% of the variance, with the first two functions explaining the highest proportion (99.6%), which will be focussed on here. Chi-square tests found the functions as significant (p<0.05) with high discriminatory ability. Based on the three discriminant functions, the stepwise DFA correctly classified 98.9% of original cases, and 98.9% using cross-validation.

Function 1 explained 98.2% of the variation and separated *C. lupus* from the other canids by its increased flesh slicing ability, with meat therefore representing a large proportion of its diet. This was combined with strong jaws, particularly at the molars, indicating the ability to capture large prey. The increased width of M2 likely improved the effectiveness of crushing complex, also aided by the increase in M1 buccal length. Thus *C. lupus* also had a greater ability to crush non-flesh foods in comparison to the other canids.

C. etruscus, C. mosbachensis and *C. arnensis* were all well separated from *C. lupus*, but grouped closer to each other, indicating more similarity on function 1 between these species than with *C. lupus*. The overall shortening of carnassial blades and weaker jaws all indicate that these canids included lower proportions of flesh into their diets, and captured smaller prey. It also indicates these canids had a decreased ability to crush non-flesh foods.

Within this group, *C. etruscus* was most separated from *C. arnensis*, with *C. mosbachensis* plotting between these species. *C. etruscus* was therefore characterised by having relatively increased flesh slicing abilities, stronger jaws, and increased molar crushing than *C. mosbachensis*, and especially more than *C. arnensis*, albeit all much reduced in comparison to *C. lupus*.

Although function 2 explained only 1.4% of the variation, it separated *C. etruscus* from the other canids, by having longer lower premolar row, with longer M1 and overall longer buccal length of the upper molar complex (p1p4L, M1L, p2p4L and M1M2L) than the other canids. Thus, combined with function 1, *C. etruscus* had an overall increased ability to crush non-flesh foods, indicating it to be more specialised towards omnivory than the other canids.

As *C. mosbachensis* plotted between *C. etruscus* and *C. arnensis* on function 1, it was apparently more able to slice flesh than *C. arnensis*, and thus incorporated a higher proportion of flesh into its diet, yet it also had more molar crushing ability. When considered with function 2, *C. mosbachensis* possessed the shortest lengths of the upper molar complex. Thus, in comparison to *C. etruscus*, *C. mosbachensis* was more carnivorous.

Function 1 also indicated *C. arnensis* as having the least flesh slicing capacity, the weakest jaws and reduced molar crushing abilities in comparison to the other canids. Interestingly, function 2 differentiated *C. arnensis* in similar fashion to *C. lupus*, indicating commonalities in molar length, although with differences in widths from function 1. This was an unexpected outcome, as it suggests that *C. arnensis* was less carnivorous but perhaps less specialised towards omnivory than *C. etruscus*.

Both *C. arnensis* and *C. etruscus* have often been considered as omnivores (Croitor and Brugal, 2010), which seems to be true to some extent here. However, *C. etruscus* was clearly better adapted to both flesh slicing and molar crushing than *C. arnensis*. For *C. etruscus*, this combination shares some affinity with *C. lupus*, although with *C. etruscus* being more adept at molar crushing and thus apparently more omnivorous.

Although the discriminant analysis clearly separated the species, it was possible that due to the body mass differences discussed in section 6.1, size rather than dietary differences was being reflected by the different measurement proportions. Therefore the differences established through function 1 may relate most clearly to body size. This possibility was explored by using Mosimann shape variables rather than raw measurements in another stepwise DFA, in order to assess variation in diet more accurately (see Chapter 4 for explanation of the method).

The stepwise DFA model based on the shape variables was created in fewer steps (6), and selected the shape variables of m1m2D, m1Ltrig, P4W, p4W, p1p4L and M1W as the best predictors of species group membership. Again, three discriminant functions were created explaining 100% of the variation, with function 1 explaining 99.1% variation and function 2 explaining 0.8% variation. Thus, together, the first two functions explain 99.8% of the variance encountered. Chi-square tests found functions 1 through 3 to be significant (p<0.05). Based on the three discriminant functions, the new stepwise DFA using the shape variables correctly classified 85.9% of original cases, and 81.9% using cross-validation.

With the effects of body size removed, both functions separated the species similarly to the original DFA using the raw measurements. Thus, function 1 separated *C. lupus* from the other Pleistocene species by having an increased flesh slicing ability, stronger jaws enabling capture of large prey, some ability to crack bone and enhanced crushing ability.

In contrast to the raw measurement DFA, more overlap between species was present, mostly between *C. etruscus*, *C. mosbachensis* and *C. arnensis* as indicated by the presence

of incorrectly attributed cases. This was also alluded to by the amount of similarity found by ANOVA in the earlier analyses. These species plotted relatively closely together, especially *C. arnensis* and *C. mosbachensis*, indicating that they were most similar to each other than to other taxa.

C. etruscus was again revealed as having comparatively less flesh slicing ability, moderately weaker jaws, and more reduced molars than *C. lupus*, but presented the reverse characteristics in comparison to *C. mosbachensis* and *C. arnensis*. Thus, it was more able to slice flesh than *C. mosbachensis*, and especially more than *C. arnensis*. *C. etruscus* also had stronger jaws for capturing somewhat larger prey than these species, as well as having more molar crushing ability than either *C. mosbachensis* or *C. arnensis*.

The differences between *C. etruscus* and *C. mosbachensis* were again clarified more by function 2, although this explained only a small proportion of the variation (0.8%) and provided much less distinct separation. *C. etruscus* was most separated from *C. mosbachensis*, indicating in the former increased molar crushing ability, as well as a longer premolar row and narrower jaws at the molars. Thus, *C. etruscus* was more adapted towards omnivory, whereas *C. mosbachensis* was more carnivorous.

It is interesting that both DFAs were similar in outcome, even when size differences were accounted for by using Mosimann shape variables. It appears either that differences in body size were not masking the effects of dietary variation in the raw measurements, or that body size cannot simply be removed from palaeodietary analysis as it is so intimately related to this aspect. The latter seems the most reasonable stance, since differences in the measurements are often dictated by body size. This will be further discussed in section 6.3.

In summary, *C. lupus* was identified correctly as a hypercarnivore, specialising in large sized prey. It also had some ability to crack bone, as well as having increased molar crushing ability, highlighting its generalist nature and flexible diet. *C. etruscus* was identified as more omnivorous than the other canids, having an increased ability to crush foods, albeit still able to slice flesh faster than *C. mosbachensis* and *C. arnensis*.

C. mosbachensis was identified as more carnivorous than *C. etruscus*, with relatively reduced crushing abilities. However, it also had a lowered ability to slice flesh in comparison to *C. etruscus*, although the opposite in comparison to *C. arnensis*.

C. arnensis had the lowest ability to slice flesh, and yet also the most reduced molars, suggesting that it occupied an intermediate position between *C. mosbachensis* and *C. etruscus* in terms of diet. It also had the weakest jaws and the lowest ability to crack bone.

In terms of Van Valkenburgh's (1988a) dietary categories (see Chapter 2) *C. etruscus, C. arnensis, C. mosbachensis* and *C. lupus* can be further differentiated by the present study than by simply being categorised as consumers of >70% meat (category 1). In particular, the diets of *C. etruscus* and *C. arnensis* in the Upper Valdarno were perhaps more varied than suggested by Cherin et al. (2013b), who placed both canids, as well as *C. falconeri*, within the same category of >70% meat. Although the dietary categories provide a guide to the level of carnivory of a species, they are perhaps too broad-brush for canids, which typically have rather generalist diets.

6.2.4. Comparison of dietary differences between the Pleistocene canids and modern species

Based on the variation found in diet between *C. lupus, C. mosbachensis, C. etruscus* and *C. arnensis*, these canids were compared to modern *C. aureus, C. adustus, C. mesomelas, C. alpinus* and *L. pictus* to see whether any dietary equivalence could be recognised between them. This is of particular interest for the extinct Pleistocene canids, as any equivalence found may allow for inferences to be made regarding palaeoecology.

Like *C. lupus,* both *L. pictus* and *C. alpinus* are hypercarnivores (Van Valkenburgh, 1989), specialising in predating large mammalian herbivores (Cohen, 1978; Macdonald, 2009). However, both *L. pictus* and *C. alpinus* have modified lower carnassials, whereby the m1 talonid basin contains a single, large, centrally positioned blade-like cusp, referred to as a 'trenchant heel' (Van Valkenburgh, 1991). In other canids, including *C. lupus*, the talonid basin contains two cusps that are sub-equal in size (Van Valkenburgh, 1991).

This trenchant heel modification effectively lengthens the m1 trigonid cutting blade, and thus allows for increased flesh slicing ability. The modification also causes concomitant changes in the M1, as well as the reduction or loss of the post carnassial molars (Van Valkenburgh, 1991).

The presence of this feature in *C. alpinus* and *L. pictus* indicates highly carnivorous diets, with a low proportion of non-flesh food incorporated, based on their lessened ability for crushing. Although *C. lupus* does not share this hypercarnivorous adaptation, it still has the

ability to slice flesh quickly, albeit not as quickly as *C. alpinus* and *L. pictus*. The main difference between *C. lupus* and these canids is therefore molar crushing ability and *C. lupus* is accordingly more able to incorporate a wider range of foods into its diet than the other two species.

C. etruscus is conventionally considered to be 'wolf-like' (Torre, 1967; Azzaroli, 1983; Garrido and Arribas, 2008), based on shared cranial features such as raised frontals and well developed sagittal crest. Although Cherin et al. (2013a) found shared cranial features between *C. etruscus* and *C. lupus*, they believed that 'wolf-like' was an oversimplification, since differences in cranial bones were present, such as the unique enlargement of the occipital region in *C. etruscus*.

Meanwhile *C. arnensis* has been considered by other authors to be either 'coyote-like' (Martinez-Navarro and Rook, 2003; Sardella and Palombo, 2007) based on shared cranial features such as a narrower muzzle, a less well-developed sagittal crest and less prominent frontals (Garrido and Arribas, 2008), or 'jackal-like' based on relative m1 and m2 length (Torre, 1967; Kurtén 1974). However, Cherin et al. (2013a) again considered this to be an oversimplification, with *C. arnensis* found to share similarities with both *C. etruscus* and *C. lupus* based on cranial traits.

Jackals are often grouped together based on dietary similarity. All have a very wide ranging omnivorous diet, which varies seasonally, including small mammals up to the size of new-born smaller sized antelope, as well as small birds, insects and fruit (Walton and Joly, 2003; Macdonald, 2009). Although it was not possible to include coyote (*Canis latrans*) into the DFA analysis, their diet is similarly varied, including lagomorphs, fruit and insects although also inclusive of larger ungulates such as wapiti (Bekoff, 1977; Gese and Bekoff, 2004).

Similar controversy exists over *C. mosbachensis*, which has been considered 'wolf-like' based on shared cranial features (Garrido and Arribas, 2008) and also 'coyote-like', based on cranio-dental features such as its well-developed m1 talonid basin indicating similar omnivorous diets (Palmqvist *et al.,* 2008). Isotopic analysis of *C. mosbachensis* remains at Venta Micena, Spain, carried out by Palmqvist et al. (2008), upheld this view, since low $\delta^{15}N$ values indicated that invertebrates and fruit were important component of its diet.

Since using raw measurements and the Mosimann shape variables produced very similar DFA models, the raw measurements only were used to examine dietary differences. The stepwise DFA model was created in 14 steps, selecting P3L, M2W, m1m2D, M1M2L,

m1Ltrig, p2p4L, P4W, M1L, p1p4L, m2L, p3p4B, p4W, p4L and m1W as the best predictors of group membership.

Eight discriminant functions were created explaining 100% of the variation. Function 1 explained 86.2% variation, with function 2 explaining only 9.6%. Together, both functions explained 95.7% of the variation. Chi-square tests found functions 1 through 8 to be significant (p<0.05) with high discriminatory ability. Based on the eight discriminant functions, the model correctly classified 96.9% of all original cases, and 96% using cross-validation.

Function 1 explained the most variation, and clearly separated all species except the jackals (*C. adustus*, *C. mesomelas* and *C. aureus*), which were indicated as having similar diets. As found in the previous DFA, *C. lupus* was indicated as having the highest flesh slicing ability, the strongest jaws, most molar crushing ability based on wide M2 and longer M1 and M1M2L, as well as having the largest p4 for some level of bone eating. None of the other recent canids were found to be closely associated with *C. lupus* on this function.

Though separated least from *C. lupus* on function 1, *C. etruscus* shares the most similarities with the modern species and echoes the wolf-like morphology discussed previously.

C. mosbachensis and *C. arnensis*, in contrast, are often considered to be more similar to coyote and jackals. Jackals were used in this analysis to represent canids with highly omnivorous diets, in lieu of available coyote comparative material. It was therefore surprising that rather than the jackal group plotting similarly to *C. arnensis* and *C. mosbachensis* on function 1 indicating some dietary similarity, instead, function 1 found both *C. alpinus* and *L. pictus* were more similar to these Pleistocene canids, with the jackals much further separated and different from *C. arnensis* and *C. mosbachensis*.

Although both wild dogs and dholes have a modified m1, the DFA only selected m1Ltrig and m1W, and excluded the potentially more diagnostic m1Ltal for these species. As stated, the trenchant heel of the talonid in both these species is diagnostic in indicating hypercarnivory. Here, the simplification of the talonid to a large, centrally-positioned single talonid cusp has effectively lengthened the trigonid cutting blade for faster flesh slicing action (Van Valkenburgh, 1991).

Thus, the similar separation of wild dogs and dholes with *C. arnensis* and *C. mosbachensis* on function 1 only suggests similarity in m1Ltrig and m1W (as well as the other correlated measurements), and does not indicate the full modification to hypercarnivory (based on

m1Ltal). The similarity in the length of the cutting blades does suggest, however, that these Pleistocene canids were more carnivorous than previously thought. This also may explain why *C. alpinus* and *L. pictus* were not grouped closer to *C. lupus* on function 1. Although they share some hypercarnivorous adaptations, *C. lupus* has relatively longer m1Ltrig, combined with stronger jaws, increased molar crushing ability and the better ability to crack bones.

As found in the previous DFAs, the Pleistocene canids grouped together, with *C. etruscus* having the highest ability to slice flesh, the stronger jaws and most molar crushing ability in comparison to *C. mosbachensis* and especially *C. arnensis*. In terms of trenchant heel modification and concomitant changes in molars, *C. mosbachensis, C. etruscus* and *C. arnensis* are all more similar to *C. lupus* in retaining a bicuspid talonid and molars.

L. pictus plotted most closely to *C. mosbachensis* on function 1, indicating a level of dietary similarity. Both are indicated as having moderately strong jaws, decreased molar crushing ability, and a reduced p4. The previous DFA indicated that *C. mosbachensis* was more carnivorous than *C. etruscus* and *C. arnensis*, and hence in terms of level of carnivory, the correspondence with *L. pictus* sits well.

However, although accounting for much less variation, function 2 clearly separated *C. mosbachensis*, and all other canids, from *L. pictus*, indicating that the modern African wild dog has a further reduction in the molar complex (narrower M2, shorter m2 and M1M2L). Thus, although *C. mosbachensis* shared some similarities with *L. pictus*, the former was clearly more adapted to incorporate non-flesh foods into its diet than the latter.

Function 2 also revealed a relationship between *C. mosbachensis* and the jackal group. *C. mosbachensis* plotted between *C. adustus*, which had the highest molar crushing abilities (wide M2, long m2 and M1M2L) on function 2, and *C. aureus* and *C. mesomelas*, which were both more similar to *C. lupus* in terms of molar crushing on function 2.

Thus, although *C. mosbachensis* was identified as being more carnivorous than the other extinct Pleistocene canids (similar in some aspects to *L. pictus*), it retained molar crushing abilities not dissimilar to modern jackals, allowing it to have a relatively more flexible diet than the modern hunting dog.

On function 1, *C. alpinus* plotted most similarly with *C. arnensis*. This was also unexpected, as *C. arnensis* has traditionally been considered more similar to jackals than to dholes. Like the hunting dog, *C. alpinus* is also a hypercarnivore, although with further reduced molars

including the loss of m3. However, function 2 highlights distinct differences between *C. arnensis* and *C. alpinus*, based on reduction in the molar complex, even more so than in *L. pictus*. Hence, although *C. arnensis* seems to share some similarities with *C. alpinus*, it retains an important ability to incorporate non-flesh foods into its diet that makes it more similar to the jackals in terms of dietary flexibility.

As discussed, although the extinct Pleistocene canids did not plot with the jackal group on function 1, more of a relationship was suggested by function 2. *C. adustus* was separated by having slightly increased molar crushing ability (wider M2, longer m2 and M1M2L), although similar to *C. etruscus* and *C. arnensis*. Both *C. aureus* and *C. mesomelas* were very similar on each function, although they were grouped by function 2 with *C. lupus* for similar molar crushing abilities.

Cherin et al. (2013a) recognised that the jackal group contained great morphological similarity, as reflected here. Nevertheless, within this group, phylogenetic relationships remain unclear. For example, *C. aureus* was considered by Gaubert et al. (2012) as more closely related to the recently established African wolf *Canis lupaster* (Rueness *et al*., 2011) (formerly known as the Egyptian jackal *Canis aureus lupaster*), and by proxy to the other subspecies of *C. lupus*, rather than closely related to *C. adustus* (Gaubert *et al.,* 2012). The view of Cherin et al. (2013a) that the definition of 'jackal-like' and 'wolf-like' is too simplistic is upheld here. Although 'wolf-like' does appear a good descriptor for *C. etruscus*, a direct analogy with modern jackals for both *C. mosbachensis* and *C. arnensis* does not fully explain the diets of either canid, since both were apparently relatively more carnivorous.

From the comparison of DFA models using both raw measurements and Mosimann shape variables, the effect of differences in body size between *C. lupus, C. mosbachensis, C. etruscus* and *C. arnensis* did not seem to alter the dietary variation present in the measurements. Body size was therefore not considered to be masking the effect of dietary variation between the species.

It is of note that the relationship between *C. arnensis* and *C. mosbachensis* with *C. alpinus* and *L. pictus* on function 1 corresponds with these species having overlapping body size ranges: *C. arnensis* with *C. alpinus*, and *C. mosbachensis* with *L. pictus* (discussed in 6.1). Size and diet are therefore difficult to disassociate, since the former hugely influential on the latter, dictating ecological niche and prey size. This relationship will be further explored in section 6.3.

6.3. Linking body mass and palaeodiet

As introduced in Chapter 3, differences in mammalian body mass are correlated with variations in life history (i.e. rates of growth, maturation and reproduction), climate (e.g. Bergmann's Rule), population density, and ecological factors relating to diet such as basal metabolic rate, prey size, hunting style and home range size.

From the reconstruction of Pleistocene canid body mass, temporal variation in size occurred in all analysed species, although it was most variable in *C. lupus* where an increasing body size trend was evident through the Devensian. From the analysis of palaeodiet, remarkable dietary stability was found in both *C. etruscus* and *C. mosbachensis*, whereas differences in climate, and the related changes in environment and biogeographical isolation, may all have influenced palaeodietary variability in *C. lupus*.

Nonetheless, carnivore community structure and resultant interspecific competition may have been equally important factors for all the Pleistocene canids. Also as outlined in Chapter 3, mammalian community structure is governed by complex interactions across the whole community between climate and the evolution and ecology of each species present. These include the evolutionary, physiological or biochemical constraints affecting each mammalian group, palaeogeographical factors controlling migration, interspecific competition within carnivore guilds, as well as the evolutionary influence between guilds (Croiter and Brugal, 2010).

The inferences on carnivore competition here are based on morphology and comparison with extant taxa, which provide the best potential analogue in the absence of evidence for specifics of behaviour, spatial or temporal separation, competitive exclusion and interspecific aggression.

6.3.1. The relationship between body mass, diet and competition

6.3.1.1. Early Pleistocene

The Early Pleistocene *C. etruscus* was a medium-sized canid, with an estimated mean body mass of 25.55 ±2.7Kg at Olivola, and 23.91 ± 1.69Kg at the Upper Valdarno sites. Both reconstructed masses overlapped in their confidence intervals, indicating close similarity between the sites.

As outlined in Chapter 3, a dietary threshold exists in carnivores at 21.5Kg. For predators above this threshold, prey generally consists solely of vertebrates, whereas below this threshold diet is often more omnivorous (Andersson, 2004b). Thus, as well as taking smaller prey, *C. etruscus*, which lay above this threshold, likely hunted prey of similar or larger size than itself. From analysis of the cranio-dental measurements, *C. etruscus* adopted a mixed feeding behaviour. It had an increased ability to crush foods and was therefore more omnivorous than both *C. arnensis* and *C. mosbachensis*. However, it also had greater flesh-slicing ability and stronger jaws than these canids, indicating that meat remained an important dietary source. Combined with its medium body size, just above the threshold weight, *C. etruscus* was likely able to hunt medium-sized prey.

Social behaviour and pack hunting developed at the Miocene-Pliocene boundary (see Chapter 2), correlated with increased encephalisation in the Caninae and with the radiation of this clade into Eurasia (Finarelli, 2008). Social behaviour was proposed for *C.* (*X.*) *lycaonoides* from Venta Micena, based on pack members apparently aiding the survival of a severely handicapped individual into adulthood (Palmqvist *et al*., 1999). In addition, extant members of *Canis* and *Lycaon* exhibit sociality. Based on this evidence, it is plausible that *C. etruscus* and *C. mosbachensis* shared this behaviour, with *C. etruscus* in particular considered a social, pack-hunting canid (Cherin *et al*., 2013b).

Pack hunting in modern canids enables the capture of large and powerful prey (Andersson, 2005), with social carnivores having better hunting success than solitary ones (Janis and Wilhelm, 1993). Thus, cooperative hunting likely aided *C. etruscus* in also capturing larger prey.

As discussed in section 6.1, the estimated body size of *C. etruscus* was within the size range of the modern *L. pictus* (mean 24.83kg, range 20-32Kg [Macdonald, 2009]). As indicated by the DFA dietary analysis, both species have some shared dietary features. However, *C. etruscus* was not as adapted towards hypercarnivory, as indicated by its retention of a bicuspid m1 talonid. In terms of crushing foods, *C. etruscus* had more similarity with jackals, in particular with *C. adustus*, although its body size was much heavier (*C. adustus* mean weight 10.8Kg, e.g. range 6.5-14Kg [Macdonald, 2009], *C. mesomelas* mean weight 8.75Kg, e.g. range 5.9-9.9Kg [Loveridge and Nel, 2004], and *C. aureus* mean weight 11Kg, e.g. range 6.5-14Kg [Macdonald, 2009]).

Based on their similar body size and likely cooperative hunting methods, the prey choices of modern *L. pictus* were used to make inferences regarding the potential prey of *C.*

etruscus. The principal prey of *L. pictus* is medium-sized antelope, of approximately 50kg in weight, although due to its cooperative hunting behaviour, larger prey up to 200kg can be targeted (Woodroffe *et al*., 2004). Prey include impala *Aepyceros melampus*, kudu *Tragelaphus strepsiceros*, Thomson's gazelle *Gazella thomsonii* as well as wildebeest *Connochaetes taurinus*. Smaller prey is also taken (<50Kg), such as dik-dik *Madoqua* spp., steenbok *Raphicerus campestris*, and duiker (tribe Cephalophini), as well as warthogs *Phacochoerus* spp. (Woodroffe *et al*., 2004).

Based on this modern analogue, *C. etruscus* at Olivola and Upper Valdarno likely hunted a wide variety of ungulates, including chamois antelope *Procamptoceras brivatense,* the deer *Eucaldoceros dicranios-ctenoides* and *Pseudodama nestii,* rupicaprine *Gallogoral meneghinii*, antelope *Gazellospira torticornis* as well as wild boar *Sus strozzi* at Olivola, and including an undetermined ovicaprine and comb-antlered deer *Eucladoceros* sp. (of small size) at the Upper Valdarno.

C. etruscus was also of similar body size to modern maned wolf *Chrysocyon brachyurus* (23 Kg [Dietz, 1985; Macdonald, 2009]), however due to lack of available comparative material, this species was not incorporated in the DFA. *C. brachyurus* is omnivorous, taking mainly fruit and small to medium-sized vertebrates such as cavy, rodents, spiny rats, armadillos, birds, reptiles and arthropods (Rodden *et al*., 2004). As *C. etruscus* was fairly omnivorous, it may have included similarly varied foods into its diet.

However, the maned wolf is a solitary hunter, with specific morphological adaptions for its tall grassland habitat (Rodden *et al*., 2004), unlike *C. etruscus*, which was a social predator with more typical wolf-like morphology.

Based on these modern comparisons, *C. etruscus* was likely able to hunt a variety of different sized prey, depending on hunting group size. Its omnivorous adaptations also allowed incorporation of other non-flesh foods, possibly including fruit.

During the Early Pleistocene, the carnivore community was larger and more diverse in comparison to the Late Pleistocene. In a period of relative climatic stability, the carnivore community was also relatively constant (Croitor and Brugal, 2010). Both the Olivola and Tasso F.U.s contained a highly diverse and abundant range of species, including many large carnivores. In terms of position within the Early Pleistocene carnivore guild, *C. etruscus* was one of the smaller carnivores, with giant short-faced hyaena *Pachycrocuta brevirostris*, jaguar-like *Panthera gombaszoegensis* (O'Regan *et al.,* 2002; Rook and Martinez-Navarro,

2010) and *Felis lunensis* (Kahlke *et al.,* 2011), of which had their first appearances at Olivola. They were joined by the extinct European cheetah *Acinonyx pardinensis*, puma *Puma pardoides,* the sabre-toothed cats *Homotherium latidens* and *Megantereon cultridens* and the wild dog-like *C. falconeri*, all of which were of larger size than *C. etruscus*.

The archaic bear *Ursus etruscus* was also present at both Olivola and the Upper Valdarno, and is considered to be of similar size to modern European brown bear (*Ursus arctos*) (160Kg for average adult male weight) (Reinhard *et al.,* 1996). However, Palmqvist et al. (2008) did not class it as a carnivore due to its morphological comparability with modern brown bear and apparently omnivorous diet. Although *C. etruscus* likely incorporated non-flesh foods into its diet, it is unlikely that *C. etruscus* and *U. etruscus* were in direct competition.

In relation to the other carnivores, however, cooperative hunting and targeting of larger herbivores by *C. etruscus* likely brought it into competitive conflict with these much larger predators. The following section will discuss these predators in terms of comparable body size, hunting strategy and target prey, in order to assess potential competitors.

P. brevirostris was extremely large in size, approximately comparable with the size of a modern female lion (e.g. 122-182Kg [Macdonald, 2009]) (Palmqvist *et al*., 2011). Morphological evidence indicates that this species was an expert bone cracker and scavenger (based on $\delta^{15}N$ stable isotopic analyses) (Palmqvist *et al*., 2008). However, its postcranial morphology suggests that it also had comparatively less predatory ability than modern spotted hyaena, and was certainly less cursorially adapted (Palmqvist *et al*., 2011). In contrast to these authors, who identified *P. brevirostris* as an obligate scavenger of carcasses killed by other large carnivores, Rodriguez et al. (2012) proposed an alternative hypothesis, that this species may have been a more active scavenger, with preferred scavenged prey of 45-180Kg, but also able to actively kill prey in the 10-1,000Kg range. Thus, preferred prey sizes may have overlapped at the smaller end with those of *C. etruscus*, with *P. brevirostris* also potentially scavenging (confrontationally or otherwise) from canid kills.

The Plio-Pleistocene genus *Homotherium* was the largest felid present in Europe, based on comparisons by Anton et al. (2005) indicating it to be similar in size to modern male lion *Panthera leo* (150-240Kg [Macdonald, 2009]). However, some debate over size of *Homotherium* exists with Meloro et al. (2007) estimating its mass during the Early

Pleistocene of Italy as 274Kg, whilst Hemmer (2002) proposed a mass of 210-400kg for *Homotherium* from Untermassfeld.

The post cranial morphology of *Homotherium* was very different from the typical hyper-robust sabre-tooths, such as the North American *Smilodon* or European *Megantereon*, with slender forelimbs indicating cursorial adaptation (Anyonge, 1996; Anton *et al*., 2005). From its gracile morphology, especially its slender forelimbs, ambush hunting was considered unlikely (Anton *et al*., 2005). *Homotherium* was further characterised by a sloping back, which was described by Anton et al. (2005) as reminiscent of hyaena in terms of its body proportions, suggesting that it was less capable of sudden acceleration and again, unlikely to be an ambush hunter. Thus *Homotherium* was possibly a social hunter, based on its gracile morphology.

Rodriguez et al. (2012) considered *Homotherium* to be the top predator in the Early Pleistocene faunal community, regularly hunting prey between 90-360Kg and possibly even larger, such as juvenile *Mammuthus* at the Early Pleistocene site Venta Micena (Palmqvist *et al*., 2003). From stable isotopic analysis at the same site, Palmqvist et al. (2008) found that *Homotherium* diet also included *Bison* sp. (52%) and *Equus altidens* (38%).

Based on this evidence, *Homotherium* from Olivola and Upper Valdarno likely targeted the largest prey such as *Leptobos* sp. (~400Kg [Meloro *et al*., 2007]) and potentially juvenile *Mastodon* sp. However, based on its large body size (above the 21.5Kg dietary threshold), *Homotherium* would have also been able to hunt prey of a similar size to itself. It is possible that conflict occurred with *C. etruscus*' hunting but *Homotherium*'s ability to take the largest prey present may have reduced competition.

A. pardinensis was considered similar to modern cheetah, although 50% larger by O'Regan et al. (2002). Using post cranial remains, Hemmer et al. (2011) estimated a body mass of approximately 100Kg. This species is thought to have been a rapid pursuit predator (O'Regan *et al*., 2002), and based on its similarity to modern cheetahs and clear cursorial adaptations, it likely hunted in open grassland environments. In terms of prey choice, modern cheetah in Africa hunt mainly medium sized antelope, Thomson's gazelle, puku and impala, also hares and new-born gazelle (Macdonald, 2009). The larger size of *A. pardinensis* would have enabled it to target prey most likely in the 45-90Kg size range, although may have also taken smaller prey (10-45Kg), as well as much larger (90-180kg) (Rodriguez *et al*., 2012). In terms of prey size range, this larger felid therefore hunted

similar sized prey as *C. etruscus*, and in a similar environment. However, its solitary hunting style, albeit cursorial, may have negated competitive interaction with the canids.

In contrast, *P. gombaszoegensis* is considered to have been an ambush predator, based on its similar postcranial morphology to extant jaguars (*Panthera onca*) (Palmqvist *et al*., 2008), although it was of larger size (modern jaguar males 57-113Kg [Macdonald, 2009]) (Turner and Anton, 1996). In comparison to other Early Pleistocene felids, it occupied a mid-range position between the smaller *Megantereon* and larger *Homotherium* (O'Regan *et al*., 2002).

From isotopic analysis of material from Venta Micena, Palmqvist et al. (2008) proposed that *P. gombaszoegensis* hunted in closed forest environments and targeted predominantly deer *Praemegaceros verticornis* (43%) and *Pseudodama* sp (38%), as well as the ovibovine *Soergelia minor* (19%). In terms of prey size, Rodriguez et al. (2012) suggested hunting of animals primarily within the 90-360Kg range. The combination of different environments occupied, hunting strategy and larger target prey would therefore have acted to minimise competition with *C. etruscus*.

P. pardoides was similar to modern puma (*P. concolor*) and although the former displays more robust postcranial morphology than the latter, a similar solitary hunting behaviour of stalking and ambush has been inferred (Rodriguez *et al*., 2012). Using modern pumas as a size guide (male pumas weigh 53-72Kg, whilst females weigh 34-48kg [Macdonald, 2009]), *P. pardoides* is considered to have been slightly larger (35-100Kg [Hemmer, 2004]), also indicating that they were somewhat smaller than *P. gombaszoegensis*. Its size would imply a preferred prey size range of 45-180kg, as well as being able to take smaller, or possibly larger sizes (Rodriguez *et al*., 2012). Although this brought it into potential competition with *C. etruscus* based on prey sizes, the differences in hunting behaviour may have served to minimise competition.

The morphology of *Megantereon* indicates that it was a solitary ambush predator, of similar size to modern leopard (*Panthera pardus*) (30-70Kg [Macdonald, 2009]) (Turner and Anton, 1997). At Venta Micena, Arribas and Palmqvist (1998) estimated body mass of 52.9Kg (range 46.1-58.1Kg), thus smaller than both *P. pardinensis* and *P. gombaszoegensis*. Isotopic analysis of *Megantereon* material from the same site indicates that this species preyed chiefly on *Equus altidens* (59%), as well as browsing and mixed feeding ungulates in closed environments such as *Praemegaceros verticornis* (31%) and *Soergelia minor* (10%), (Palmqvist *et al*., 2003; 2008). Based on its size, Rodriguez et al. (2012) inferred a target

prey size of 90-360Kg, possibly extending down to 45Kg. In light of their different preferred environments and hunting styles, it therefore seems less likely that *C. etruscus* and *Megantereon* were in direct competition for the same prey.

Although competition from larger felids must have exerted some level of pressure on *C. etruscus*, it might be expected that interaction between the different species of canid at the Upper Valdarno caused more conflict. However, based on the analyses undertaken during the present study, the diet of *C. etruscus* apparently did not alter following the arrival of *C. falconeri* and *C. arnensis* during the Tasso F.U. However, there does seem to be a slight reduction in mean body mass from Olivola (25.55 ±2.70Kg) to Upper Valdarno (23.91 ± 1.69Kg), although both estimates overlap in their variation.

C. falconeri was a hypercarnivorous canid (Martinez-Navarro and Rook, 2003), larger than *C. etruscus*. In order to understand predator-prey relationships, Rodriguez et al. (2012) grouped the wild dogs together as the *Lycaon* group defined by Martinez-Navarro and Rook (2003), with *L. falconeri* (= *C. falconeri*) - *L. lycaonoides* (= *C.* (*X.*) *lycaonoides*) - *L. pictus* forming the wild dog lineage, and representing Pleistocene chronospecies. Preferred prey choices for the Early Pleistocene *C. falconeri* and later *C.* (*X.*) *lycaonoides* were inferred from the slightly smaller modern *L. pictus*, indicating that both Pleistocene species were social hunters, and likely hunted prey of a wide size range (90-360Kg), based on their group hunting ability (Rodriguez *et al*., 2012). Smaller sized prey of 10-45kg and 45-90kg would also have represented a significant proportion of its diet (Rodriguez *et al*., 2012).

Although able to take larger prey than *C. etruscus*, both canids overlapped in their small and medium prey choices, and thus competitive interaction was likely very common. However, based on the apparent dietary stability of *C. etruscus* and relatively low levels of broken and worn teeth, it seems that effective resource partitioning occurred between the canids, perhaps due to highly abundant prey. In light of this, the slight reduction in body mass may have been in response to the presence of a larger canid, which acted to constrain *C. etruscus*, thereby forcing differentiation of resources to some degree.

C. etruscus was larger than *C. arnensis*, which had estimated body mass of 17.94 ±1.73Kg for the Upper Valdarno. This mass was below the established 21.5Kg dietary threshold, and thus implies that *C. arnensis* did not hunt prey larger than itself, an observation supported by the presence of relatively weaker jaws, as revealed in the dietary analysis. *C. arnensis* was less able to slice flesh quickly than the other canids studied here and was more

omnivorous than *C. mosbachensis* but less so than *C. etruscus*. Thus, it is assumed to have hunted small prey, with a lower input of non-flesh foods than *C. etruscus*.

As discussed in section 6.1, *C. arnensis* was of similar body size to the alpine dhole *Cuon alpinus* (mean 16.93Kg, with a range of 10-20Kg [Cohen, 1978]), the Ethiopian wolf *Canis simensis* (mean 15.6Kg, with a range of 11.2-19.3Kg [Sillero-Zubiri and Gottelli, 1995]) and the coyote *Canis latrans* (mean 14.25Kg, with a range of 7-20Kg [Bekoff, 1977]), implying similar prey size selection for *C. arnensis*.

Although more hypercarnivorous than *C. arnensis*, *C. alpinus* mainly hunts vertebrate prey in social groups of up to 12 members (Cohen, 1978), preferring medium and large-sized ungulates between 31-175Kg (Karanth and Sunquist 1995). Diet varies seasonally and regionally, with sambar, wild and domestic cattle, chital and lagomorphs preyed on in India, reindeer and wild sheep and goats in Russia, and sambar, red muntjac, east Asian porcupine, insects, birds, reptiles and vegetation consumed in Thailand (Durbin *et al*., 2004).

Cooperative hunting therefore allows *C. alpinus* to hunt larger prey than the carnivore dietary threshold of 21.5Kg would dictate, including juveniles of much larger herbivores. As discussed, based on the dietary threshold, *C. arnensis* at the Upper Valdarno likely hunted small mammals up to ovicaprine size. However, from its size similarity with *C. alpinus*, cooperative hunting (as inferred by Kahlke et al. [2011]) may have also enabled *C. arnensis* to target prey larger than itself. Nevertheless, since the dentition of *C. arnensis* suggests that it was apparently more omnivorous than *C. alpinus*, it was perhaps most similar to *C. latrans*, with which it is often compared (see section 6.2) in terms of its inferred diet. The coyote is an opportunistic and generalist hunter, with a highly varied diet including deer, lagomorphs, fruit and insects (Bekoff, 1977; Gese and Bekoff, 2004). Larger ungulate carcasses are often scavenged (Gese and Bekoff, 2004), and hunting can be both cooperative for larger prey, and individual (Gese and Bekoff, 2004).

Although of similar size, it seems unlikely that prey choices of *C. arnensis* were comparable to those of modern *C. simensis*, since the latter has a highly specialised diet due to its restricted afro-alpine high latitude habitat. *C. simensis* almost exclusively hunts rodents, in particular the giant molerat, Blick's grass rat and the black-clawed brush-furred rat (Sillero-Zubiri and Gottelli, 1995), as well as occasional predation of rock hyrax, and juvenile duiker and reedbuck (Sillero-Zubiri and Marino, 2004). Although *C. arnensis* undoubtedly hunted similar small sized prey, its diet was probably more varied due to its less restricted habitat.

Furthermore, although *C. simensis* live socially of between 3-13 adults (Sillero-Zubiri and Marino, 2004), they hunt individually (Sillero-Zubiri and Gottelli, 1995), a behaviour that cannot be ruled out for *C. arnensis*.

Considering the presence of two larger competing canids in the form of *C. etruscus* and *C. falconeri*, access to smaller prey may have been more realistic for *C. arnensis*. In terms of other carnivores, it is possible that *C. arnensis* and the small wild cat *Felis lunensis* may also have competed over access to small prey, although the preference of the latter for woodland edge environments and its ambush predation style may have minimised interactions.

In an analysis of body size ratios between the sympatric canids in the Upper Valdarno (*C. falconeri, C. etruscus and C. arnensis*), Garcia and Virgos (2007) found the canid guild to be evenly spaced and in equilibrium, which suggests that effective resource partitioning occurred between the canids, based on their evenly spaced body sizes.

Both the Early Pleistocene carnivore and herbivore communities have been described as ecologically stable (Croitor and Brugal, 2010), relating to relatively stable temperate conditions. These conditions engendered a highly productive environment in the Early Pleistocene (Meloro *et al*., 2007), and as the abundance of prey is controlled by available resources, a highly diverse and large body sized carnivore community could be supported. Although the Upper Valdarno witnessed elevated predator-prey ratios, stemming from the substantial number of newly-arrived carnivores, the lack of palaeodietary variability in *C. etruscus*, the differences in body mass between the various large carnivores and low levels of tooth breakage and wear in both *C. etruscus* and *C. arnensis*, suggests that resources were adequately partitioned.

6.3.1.2. Late Early – Middle Pleistocene

The estimated body mass for *C. mosbachensis* was 22.50 ±1.62Kg (in Britain: 22.47 ±1.69Kg, mainland Europe: 22.22 ±1.67Kg), slightly smaller than *C. etruscus* although within its lower range. This body mass estimate places *C. mosbachensis* above the dietary threshold of 21.5Kg, and implies that it was able to hunt prey large than itself, aided by its cooperative hunting style.

Based on the dietary analysis conducted here, *C. mosbachensis* had relatively weaker jaws and slicing ability than both *C. etruscus* and *C. lupus*, although cranio-dental measurements

suggest that its diet was relatively more carnivorous than the earlier Pleistocene canids based on lower molar crushing ability.

C. mosbachensis was similar in size to *C. etruscus, C. brachyurus* (23Kg [Dietz, 1985; Macdonald, 2009]) and *L. pictus* (24.83Kg, e.g. range 20-32Kg [Macdonald, 2009]) and larger than both coyote and jackals. Data from modern *L. pictus* and *C. brachyurus* was therefore used to infer the size of prey hunted by *C. mosbachensis*. As previously discussed, *L. pictus* predominantly hunts medium-sized ungulates around 50kg but larger prey up to 200kg can be targeted cooperatively (Woodroffe *et al*., 2004). Although *L. pictus* is more adapted to hypercarnivory, the similarity in body size and thus prey size choices, as well as hunting behaviour may be more comparable to *C. mosbachensis* than *C. brachyurus*, with the latter having a more omnivorous diet and solitary hunting behaviour, predating small and medium sized mammals.

The similar size and inferred prey choices to *C. etruscus* indicate that *C. mosbachensis* may have occupied a similar ecological niche and maintained a similar position within the carnivore community. However, unlike *C. etruscus*, *C. mosbachensis* was the smallest canid present, with only the larger *C.* (*X.*) *lycaonoides* representing an additional canid competitor. Thus in terms of potential prey, *C. mosbachensis* likely targeted a range of ungulates of medium to large size, with the latter aided by cooperative hunting. From the prey recorded from Untermassfeld, prey may have included deer such as *Cervus s.l. nestii vallonnetensis* and *Capreolus cusanoides* as well as *Equus wuesti* and *Sus scrofa.* The Eurasian beaver *Castor fiber* may also have been hunted, based on patterns of modern wolf predation (Jedrzejewski *et al*., 2000).

The carnivore community of the late Early Pleistocene (slightly older than 1Ma for Untermassfeld [Kahlke *et al*., 2011]) was broadly similar to that of the earlier Pleistocene, although with an overall reduction in canid diversity through the loss of *C. etruscus* and *C. arnensis*. At Untermassfeld, *C. mosbachensis* coexisted with *P. brevirostris*, as well as numerous larger felids such as cheetah-like *Acinonyx pardinensis pleistocaenicus, P. gombaszoegensis, P. pardoides, Homotherium latidens,* the dirk-toothed *Megantereon cultridens adroveri* and lynx *Lynx issiodorensis* (Kahlke and Gaudzinski, 2005). Again, the presence of bear (*Ursus rodei*) is not thought to be a significant competitor.

The competitive interactions of these species have previously been discussed with regards to *C. etruscus*. As *C. etruscus* and *C. mosbachensis* had similar ecological niches, competition between these species and *C. mosbachensis* was likely similar, particularly

from the other open environment predators such as *P. brevirostris, H. latidens, A. pardinensis pleistocaenicus, P. pardoides, M. cultridens adroveri* and *L. issiodorensis*, which overlapped in target prey sizes.

L. issiodorensis was comparatively more robust then modern lynx (*Lynx lynx*), with a larger head, longer neck and shorter limbs, as well as being of slightly longer body length (Kurtén, 1978). Nonetheless, modern lynx was considered best analogue for this species (Rodriguez *et al*., 2012). Modern lynx is 8 - 31Kg (Macdonald, 2009) in size, and in comparison to the large felids dominating the late Early Pleistocene, *L. issiodorensis* was a much smaller cat. Based on its modern relatives, *L. issiodorensis* was likely an ambush predator in closed woodland environments, hunting small ungulates of 10-45kg, with smaller or possibly slightly larger mammals also included in diet (Rodriguez *et al*., 2012). Despite the overlap in prey size choices, interaction between *C. mosbachensis* and *L. issiodorensis* was probably rare on account of their different environmental preferences and hunting styles.

As with the Early Pleistocene, the larger canid present, *C.* (*X.*) *lycaonoides*, likely presented the highest level of competition for *C. mosbachensis*, based on similar hunting behaviour and highly overlapping preferred prey sizes. Like its predecessor *C. falconeri*, *C.* (*X.*) *lycaonoides* was also hypercarnivorous and was larger in size than the modern wild dog *L. pictus* (Martinez-Navarro and Rook, 2003). Body mass estimates from Venta Micena indicate that *C.* (*X.*) *lycaonoides* was 29.7Kg (range 16.4-53.8Kg) or even 36.7Kg (range 18.5-72.8Kg) in weight (Palmqvist *et al*., 2002).

Isotopic analysis at Venta Micena further highlighted that *C.* (*X.*) *lycaonoides* preferred open environment prey such as *Equus altidens* (58%), although isotopic evidence suggested hunting of browsing herbivores such as *Hemitragus albus* (30%) and *Pseudodama sp* (12%) was equally common (Palmqvist *et al*., 2003; 2008). Thus, *C.* (*X.*) *lycaonoides* was considered to be the most versatile predator in the late Early Pleistocene community (Palmqvist *et al*., 2008).

The early Middle Pleistocene large carnivore community in Britain contained many similar elements to the Early Pleistocene, although with the addition of spotted hyaena *Crocuta crocuta* (the first evidence of this species occurring at West Runton [Turner, 1995a]) and lion *Panthera leo* (first appearing at Pakefield, [Lewis *et al*., 2010]). However, based on the carnivores present at West Runton, the overall diversity of large felids seems to have reduced by this time, with only *H. latidens*, *P. gombaszoegensis* and cf. *Lynx* sp. present, a

single bear species (*Ursus* sp.) together with other small cats such as *Felis* cf. *lunensis* and a second, smaller *Felis* sp. (Stuart and Lister, 2010).

As no temporal differences were found in *C. mosbachensis* diet between the late Early Pleistocene and the early Middle Pleistocene, the turnover in the carnivore community apparently did not cause any response in this species. Although the only evidence of *C.* (*X.*) *lycaonoides* in Britain is at Westbury (Bishop, 1982), there is no reason to believe that the larger canid may not have also been present throughout the early Middle Pleistocene in Britain. Hence, competition from the larger canid had a continual constraining effect on *C. mosbachensis* that may have confined it in its prey choice and promoted dietary stability.

Compared with modern African *C. crocuta* (body size 45-80Kg [Hayward, 2006]), Pleistocene *C. crocuta* was larger, particularly during the Late Pleistocene (Turner, 1981), with early Middle Pleistocene specimens from West Runton and Westbury of similar proportions to their Late Pleistocene counterparts at Kents Cavern (Turner, 1999). Pleistocene *C. crocuta* likely actively hunted as well as scavenged large sized prey. From a composite study of spotted hyaena diet in African national parks, Hayward (2006) found that very few prey species were neglected in this species' environment, although a size preference of 56-182Kg existed. Modern spotted hyaena diet therefore overlaps with those of all other large carnivores present, namely lion, leopard, cheetah and wild dog (Hayward, 2006). A similar ecological niche can reasonably be inferred for Pleistocene *C. crocuta*, and the addition of this carnivore to the community would have increased competition with the other members of the large carnivore guild. In particular, *C. crocuta* would have been in competition with the larger scavenger *P. brevirostris* at West Runton. As a wide range of prey would have been targeted, it is also possible that carcasses were scavenged from *C. mosbachensis* kills or similar prey actively hunted. *C. crocuta* is well-adapted to cracking bone using its enlarged and round P3, enabling it to access marrow unavailable to other canids, as well as to consume fully entire carcasses (Kruuk, 1972; Van Valkenburgh, 1991).

Based on studies of wild dog and spotted hyaena interactions in Africa by Creel and Creel (1996), the predation of wildebeest by both species led to extensive dietary overlap, although wild dogs supplemented their diet with smaller impala and gazelles, and hyaena also hunted other large prey such as zebra and gemsbok. Interference competition from hyaenas affected wild dogs, although this was highly dependent on environment type. Competition was high in open grassland areas with high visibility, and low in wooded shrub areas (Creel and Creel, 1996). The density of hyaenas was also important, as wild dogs were

able to defend kills from small numbers of hyaenas but lost out when numbers were high (Creel and Creel, 1996).

P. leo was generally larger than its modern counterpart during the Pleistocene (Lewis *et al*., 2010) (modern males 150-240Kg [Macdonald, 2009]). Modern lion prefer prey between 190-550Kg (Hayward, 2006), including young African elephant, buffalo, eland, giraffe and kudu, wildebeest, kongoni, Thomson's gazelle, topi, warthog, zebra (Haas *et al*., 2005). In the absence of preferred larger prey, smaller mammals such as gemsbok and porcupines may also be hunted (Haas *et al*., 2005). Based on their modern counterparts, Pleistocene lions were likely also social, since modern lions are the most social of all felids, living in large prides consisting of 3-10 adult females and 2-3 adult males (Macdonald, 2009).

From the herbivorous species present at West Runton, potential prey may have included the young of *M. trogontherii, Bison* cf. *schoetensacki* as well as giant deer *Praemegaceros verticornis* and *Megaloceros savini*. The young of the rhinoceros *Stephanorhinus hundsheimensis* may also have been targeted.

In terms of competitive interaction, based on *C. mosbachensis'* modern ecological analogue of wild dog, competitive interaction may have been minimal, since African wild dogs and lion rarely interact and wild dogs commonly leaving active lion areas alone (Creel and Creel, 1996). Notably, lions also preyed upon wild dogs in Kruger National Park (Creel and Creel, 1996). Hence, *C. mosbachensis* and lion may have overlapped in some prey but the risk of lion confrontation may have been too high for the canids.

The Middle Pleistocene saw the replacement of machairodont felids and *P. brevirostris* by their ecological counterparts of lion and spotted hyaena respectively (Turner, 1995a). In Britain the last appearance of *P. gombaszoegensis* was at Swanscombe (MIS 11) (Turner 1995a) although this is based upon a humerus that has recently been reassigned to *Homotherium* by S. Parfitt (D. Schreve, pers. comm.). The persistence of sabre-toothed cats after the Anglian is an interesting support for the finds of *Homotherium* from Late Pleistocene deposits at Kents Cavern in Devon and Robin Hood's Cave at Creswell Crags, Nottinghamshire (McFarlane and Lundberg, 2013), as well as a *Homotherium* mandible from the North Sea that has been radiocarbon dated to 28,000 yr BP by Reumer et al. (2003). Although there is no confirmed record of *P. gombaszoensis* beyond MIS 11 in Britain, which may in itself no longer be accurate**,** sabre-toothed cats may have continued (or even re-immigrated from North America) into the Late Pleistocene in Britain, which will be discussed in the following section.

In summary, the medium sized *C. mosbachensis* was one of the smallest large carnivores present in the community, likely occupying a broadly similar niche to that of the Early Pleistocene *C. etruscus* based on their similar size. The carnivore guild of the late Early Pleistocene was similar to that of the Early Pleistocene, however, important structural changes in the community occurred from the Early to Middle Pleistocene transition, with the extinction of solitary hypercarnivorous felids, and the increased importance of social hunters with broader diets (Croitor and Brugal, 2010).

The gradual reduction in large predators apparently did not cause variation in the diet of *C. mosbachensis* prior to the MIS 12 Anglian glaciation, indicating stability for the medium-sized canid. It is possible that a decrease in hypercarnivores enabled *C. mosbachensis* to become more carnivorous than *C. etruscus* and *C. arnensis*.

As with *C. etruscus*, *C. mosbachensis* was likely constrained by the presence of larger carnivores, in particular larger canids, with active partitioning and differentiation of resources and all available ecological niches filled. The disappearance of *C.* (*X.*) *lycaonoides* by the end of the early Middle Pleistocene (Martinez-Navarro and Rook, 2003) pre-dates the last occurrence of *C. mosbachensis*, which is present in Britain until MIS 9. The loss of the larger canid would have opened up their ecological niche, and likely lessened the competitive pressure on *C. mosbachensis*. Unfortunately a lack of material of Late Middle Pleistocene age (MIS 11-9) makes inferences about the effect of this competitive release difficult.

6.3.1.3. Late Middle Pleistocene - present

The estimated body mass for Pleistocene *C. lupus* was 35.81 ± 1.59Kg (for Britain: 36.25 ± 1.59Kg, for mainland Europe: 34.23 ± 1.64Kg). Compared to the earlier Pleistocene canids, Pleistocene *C. lupus* was up to a third larger, making it distinctly different in its prey choices and competitive interactions with other large predators. However, unlike the earlier Pleistocene canids, which appear relatively stable in body size through time, temporal variation in body size was found between MIS 7, 5a and 3: MIS 7 at an estimated 34.03 ± 1.73Kg, MIS 5a at 39.85 ± 1.64Kg and MIS 3 at 35.40 ±1.63Kg. These variations in body size are correlated with temporal variation in diet, which itself was related to differences in climate, and in particular openness of the environment, prey diversity and competition.

The estimated body sizes are all within the size range of modern *C. lupus* (41.33Kg, range 18-80Kg [Mech, 1974]). Thus, based on similar hunting behaviour and size, inferences about prey choices can be inferred from the modern counterpart. Modern *C. lupus* hunts a wide range of prey, with elk (*Alces alces*) the largest animal taken (400-800Kg [Macdonald, 2009]), as well as other large ungulates such as wapiti (*Cervus canadensis*) (240-454Kg [Macdonald, 2009]), reindeer (*Rangifer tarandus*) (91-272Kg [Macdonald, 2009]) and red deer (*Cervus elaphus*) (76-111Kg in Scotland [Clutton Brock and Albon, 1983] but highly variable regionally). Other medium and small prey taken include wild boar (*Sus scrofa*) (50-200Kg [Macdonald, 2009]), white-tailed deer (*Odocoileus virginianus*) (18-136Kg [Macdonald, 2009]), roe deer (*Capreolus capreolus*) (17-23Kg [Macdonald, 2009]), Eurasian beaver (*Castor fiber*) (11-30Kg [Macdonald, 2009] and hare *Lepus* sp. (1.2-5Kg [Macdonald, 2009]).

From analysis of cranio-dental measurements, late MIS 7 *C. lupus* was less adapted for fast flesh slicing and more adapted for non-flesh food crushing, combined with comparatively weaker jaws than its MIS 5a and modern counterparts. Thus late MIS 7 *C. lupus* was certainly able to hunt prey much larger than itself, aided by cooperative hunting, but despite its own dramatic increase in body size and in view of the presence of much larger predators, it may have avoided tackling the very large herbivores that modern wolves can bring down.

The large carnivore community of the late Middle Pleistocene was much less diverse in comparison to the Early and early Middle Pleistocene. By late MIS 7 (the Sandy Lane MAZ of Schreve, 2001a), *P. leo* was often common, with apparently fewer numbers of *C. crocuta*, and rare leopard (*P. pardus*), the last restricted to upland sites such as Pontnewydd Cave and Bleadon Cave (Schreve, 2001a). Other smaller carnivores were also present, such as red fox (*Vulpes vulpes*) and wild cat (*Felis sylvestris*).

Brown bear (*Ursus arctos*) was also present, and importantly, there is evidence of a new competitor in the form of *Homo neanderthalensis*, which was ubiquitous across southern and central Britain. The reduction in diversity of large carnivores, combined with a substantially increased body size, allowed *C. lupus* to occupy a more prominent position in the carnivore guild in comparison to both *C. etruscus* and *C. mosbachensis*.

Prey diversity had also decreased compared to the earlier Pleistocene, with grassland species dominating during late MIS 7: in particular a late morphotype of steppe mammoth (*Mammuthus trogontherii*), abundant horse (*Equus ferus*), bovids such as *Bos primigenius*

and *Bison* cf *priscus*, red deer (*Cervus elaphus*) and hare (*Lepus* cf. *timidus*). Indicators of woodland habitats were much less common except in upland areas, but included straight-tusked elephant (*Palaeoloxodon antiquus*), together with wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*) and Eurasian beaver (*Castor fiber*).

Pleistocene *P. pardus* was likely similar to its modern counterpart. Modern leopards are highly adaptable, solitary ambush predators of 30-70Kg in size, with a varied diet including reptiles, birds, small mammals and medium sized antelopes (Macdonald, 2009). They are also known to hunt other carnivores such as bat-eared foxes and cheetah (Macdonald, 2009). Thus as well as targeting similar prey, it is possible that neonate wolves were at risk from leopard predation, as well as from lions.

The earliest appearance of *U. arctos* in Britain was during MIS 9, replacing the cave bear *U. spelaeus* that was characteristic of the Swanscombe MAZ of MIS 11 (Schreve, 2001a). Pleistocene *U. arctos* was more carnivorous, as well as larger than its modern counterpart (modern males 135-545Kg [Macdonald, 2009]) (Baryshnikov and Boeskorov, 2004). Although more omnivorous than their Pleistocene counterparts, foraging for plants, tubers and berries, brown bears also often prey upon winter-weakened or old aged ungulates such as red deer (*Cervus elaphus*) and North American moose or Eurasian elk (*Alces alces*), as well as their calves (Pasitschniak-Arts, 1993). Carrion of large ungulates is consumed, as well as small mammals such as ground squirrels (*Spermophilus*), marmot (*Marmota*), lemming (*Lemmus*), collared lemming (*Dicrostonyx*) and voles (*Clethrionomys*) (Pasitschniak-Arts, 1993).

Based on the ungulate prey and carrion utilisation of modern brown bears, competition was likely between *U. arctos* and the other carnivores present based on targeting similarly medium and large sized prey. However, *U. arctos* may also have had a more varied diet during interglacials, thereby relieving competitive pressure during more climatically favourable periods.

After its earliest appearance in Britain during the early Middle Pleistocene, *C. crocuta* had only scarce appearances in Britain during MIS 9 and MIS 7 (although taphonomic factors must be taken into consideration, since carnivores occur at low density in the landscape and few of the sites studied from the late Middle Pleistocene are cave sites where carnivores would be expected to be more common). The species increases in abundance into the Late Pleistocene (Turner, 1995a) and is the dominant predator in the MIS 5e interglacial and MIS 3, the Middle Devensian.

As discussed previously, based on its modern counterpart, Pleistocene *C. crocuta* likely hunted and scavenged large prey such as *B. primigenius*, *B.* cf. *priscus* and *E. ferus* as suggested by Turner (2009), as well as *C. elaphus.* Thus, *C. crocuta* most likely scavenged from all other carnivores present, as well as overlapping with them in its prey choices.

Although both *P. pardus* and *C. crocuta* may have exerted some competitive pressure on *C. lupus* during late MIS 7, as the most abundant social carnivore, *P. leo* would likely have been the major competitor with *C. lupus*.

As mentioned in section 6.2, the late MIS 7 lion was much larger in size compared to its modern counterpart (Schreve, 1997). Modern lion body size ranges between 122-240Kg, and combined with their social hunting behaviour, they can take large ungulates such as gazelle, zebra, antelope, giraffe and wild pig, as well as juveniles of elephant and rhinoceros (Macdonald, 2009). Thus the larger MIS 7 lions were likely able to hunt the largest prey available, including all of the major large herbivores (horse, aurochs, bison, red deer, giant deer) as well as juveniles of steppe mammoth, straight-tusked elephant and woolly rhinoceros. With the exception of the proboscideans and rhinoceros, the prey choices of *P. leo* and *C. lupus* in late MIS 7 likely overlapped to a substantial degree. However, wolves likely more often targeted small prey, such as ground squirrel and hare, in comparison to lion, whom in modern environments only take small prey (such as gemsbok and porcupine) when large ungulates are absent (Haas *et al*., 2005).

The advent of Neanderthals in Britain, first noted during MIS 8 (Bridgland, 1998; Schreve *et al*., 2002), represents a new, major predator in the landscape. Multiple carbon and oxygen stable isotopic analyses of Neanderthals from between 120-37Ka in Europe by Richards and Trinkaus (2009) found that the Neanderthals had similar isotopic signatures to the large carnivores present (except cave bears), indicating that all their protein was derived from large terrestrial herbivores and implying that they were both top predators and active hunters.

From Late Pleistocene sites such as Taubach (~MIS 5e) (Bratlund, 1999) and Salzgitter Lebenstedt (~MIS 5-3) in Germany (Gaudzinski and Roebroeks, 2000) and Baume-Vallée in France (~MIS 5-4) (Daujeard *et al*., 2012), typically hunted prey included Merck's rhinoceros, bison and aurochs, reindeer, equids and cervids, depending on location and climatic conditions. All age classes were hunted at Baume-Vallée (Daujeard *et al*., 2012), whilst specific targeting of adult reindeer at Salzgitter Lebenstedt occurred for marrow processing (Gaudzinski, 2000).

The range of prey size hunted, combined with the focussed predation on individual species and age classes indicates that Neanderthals were probably capable of hunting any size animal, which thus made them a direct competitor with all the large carnivores present.

In summary, the presence of larger predators including Neanderthals likely exerted competitive pressure on *C. lupus* during late MIS 7. However, the incorporation of non-flesh foods into the diet during this interglacial allowed *C. lupus* a degree of flexibility, and enabled it to better resist high levels of competition.

Both hyaena and lion constrained *C. lupus*, in terms of ecology and body size, by excluding certain prey via resource partitioning. From the low number of broken teeth and high number of only slightly worn teeth, *C. lupus* does not appear to have been rapidly and fully consuming carcasses, which would be indicative of either low resources or high competition for food. Instead it seems that although competition was likely high from lion and hyaena, prey was sufficiently abundant.

As previously discussed, the carnivore community and prey diversity present during MIS 5a were very different to those seen in both MIS 7 and 3. The only carnivore larger than *C. lupus* in MIS 5a was an exceptionally large form of *U. arctos* (Currant and Jacobi, 2001). The main prey species present were *Bison priscus*, *Rangifer tarandus* and *Lepus timidus*, with *Microtus oeconomus* the only small mammal recorded. The last may have been predated by wolf but is likely to have been targeted more by Arctic fox. Both *C. crocuta* and *P. leo* were absent from Britain at this time, as well as Neanderthals.

The very low diversity and probable seasonal availability of prey likely meant that prey choices between *U. arctos* and *C. lupus* doubtless heavily overlapped, and combined with the paucity of plant resources in MIS 5a, the bear would have had little option but to become highly predatory. The comparatively larger body mass estimate for *C. lupus* from MIS 5a (39.85 ±1.64Kg) would have enabled wolves to hunt larger prey than their MIS 7 and 3 counterparts, making even adult *B. priscus* (estimated 672 ±152 Kg at Banwell [Collinge, 2001]) a more attainable target at this time.

From the dietary analysis conducted here, MIS 5a *C. lupus* was better adapted to fast flesh slicing than non-flesh food crushing, as well as possessing enhanced bone cracking ability and broader jaws for manipulating large prey. As discussed, the ability to slice flesh quickly is related to low resource environments and high levels of competition (Section 6.2), which would have come both from the large *U. arctos* and from other wolves. There is also some

evidence of wolf-wolverine competitive aggression, often resulting in wolves killing the wolverine (Ballard *et al*., 2003).

In summary, competition for very limited resources is considered to have been high during MIS 5a, despite the reduction in predator diversity in contrast to MIS 7 and 3. The lack of spotted hyaena was likely very influential for *C. lupus*. Without an immediately larger carnivore positioned above wolf in the community, constraints on both body size and ecology were eased, resulting in larger size and broadening of the dietary niche.

However, the unique climatic and palaeogeographical conditions of MIS 5a doubtless affected *C. lupus*, as previously discussed. Cold climatic conditions may have led to a Bergmannian response towards increased body size, rather than it being simply the result of a reduced carnivore guild. Furthermore, the harsh climatic conditions, apparent island isolation and limited vegetational availability resulted in reduced prey and other resources and led to increased competition for food, novel dietary adaptations (notably bone consumption) and high incidences of tooth breakage and wear.

It is of note that although *C. lupus* increased in size at this time and adapted its diet to prevailing conditions, these differences were not perpetuated in Britain for the remainder of the Pleistocene once the landmass became reconnected to the continent and climate ameliorated into MIS 3. Thus the differences observed were driven by the unique combinations of climatic, environmental and palaeogeographical conditions, and highlight the adaptability of *C. lupus* to extreme conditions.

The body mass estimate for *C. lupus* from the Middle Devensian, MIS 3, was 35.40 ±1.63Kg, which was within range of the estimate from MIS 7. Based on the analysis of diet, MIS 3 *C. lupus* was also more similar to MIS 7 in terms of being more adapted to crushing non-flesh foods than fast flesh slicing, as well as having comparatively weaker jaws than MIS 5a *C. lupus*. Thus, higher proportions of non-flesh foods were incorporated into its diet, with prey size choices similar to those of MIS 3. None of the morphological adaptations seen in MIS 5a were still present by MIS 3.

The carnivore community and prey diversity of MIS 3 was similar to MIS 7, albeit characterised by different climatic conditions. Although MIS 3 is within a cold stage, it is nonetheless the warmest part overall, which may explain comparability with some elements of MIS 7. *P. leo* and *C. crocuta* were both present, as well as *U. arctos* (smaller than in MIS 5a; estimated as 345 ±105Kg at Kents Cavern [Collinge, 2001]), while large

herbivores indicative of open environments were dominant, such as *Mammuthus primigenius*, *C. antiquitatis*, *B. priscus*, *Equus ferus*, *M. giganteus*, *R. tarandus* and *Lepus* sp, attributed to the Pin Hole MAZ (Currant and Jacobi, 2001, 2011).

From analysis of dietary isotopes, Bocherens et al. (2011) found that Late Pleistocene (MIS 3) *U. arctos* from the Belgian Ardennes was in competition with *C. crocuta* based on overlapping prey choices but as the larger animal, brown bear was able to minimise competitive pressure by hunting larger prey unavailable to hyaena. However, after the Last Glacial Maximum, c. 20 ka, dietary isotopes analysed from sites of the northwestern Alpine foreland (Jura Mountains, France-Switzerland border) suggest that *U. arctos* became more herbivorous, exploiting a similar ecological niche to the recently extinct cave bear (*Ursus spelaeus*) (Bocherens *et al*., 2011). However, the regional and subsequent habitat difference between these compared areas is large, with brown bear diet varying enormously depending on latitude and habitat.

By the Late Pleistocene, *C. crocuta* had increased in abundance in Britain and would have been a formidable competitor for *P. leo*, *U. arctos* and *C. lupus*, more so than during MIS 7. The Late Pleistocene *C. crocuta* was larger and more robust than its modern counterpart based on longer skull basal lengths and shortened limbs, indicating a possibly less gracile habit (Turner, 1981). Based on the overall larger size of *C. crocuta* during MIS 3, large and medium-sized prey was likely hunted and scavenged, including *B. priscus*, *E. ferus*, *M. giganteus* and *R. tarandus*, as well as including larger prey such as woolly rhinoceros, *C. antiquitatis. S*cavenging from *P. leo*, *U. arctos* and *C. lupus* may also have occurred.

The prey choices of *P. leo*, *C. crocuta* and *C. lupus* thus probably overlapped. From the large numbers of juvenile *C. antiquitatis* and *M. primigenius* remains gnawed by *C. crocuta* in Kents Cavern, hyaenas also utilised the largest prey present. However, differentiation between prey choices likely occurred between hyaenas and lions based on hunting ability. In comparison to lions, which pursue selected prey at speed (~50 Km/h) up to 50-100m (Kruuk and Turner, 1967), hyaena chase for limited distances (Cooper, 1990). Hence, by being better adapted for pursuit, lions may have been able to tackle a wider range of ungulate prey.

Specimens of lion from Pin Hole Cave and Kents Cavern were considered to be cave lion (*Panthera spelaea*) as opposed to *P. leo* by Stuart and Lister (2011). There is some debate, highlighted by Burger et al. (2004), as to whether both lion groups should be taxonomically

combined within *P. leo* (Kurtén 1968; Turner and Anton 1997), or rather whether they should be separated into *P. spelaea* and *P. leo* (e.g. Baryshnikov and Boeskorov 2004).

Although both species have shared morphological features, *P. spelaea* has often been considered a subspecies of lion (Kurtén, 1968, *contra* Turner, 1984). *P. spelaea* had more inflated bullae and braincase, more arched zygomata and differences in the upper carnassials, whereas *P. leo* has a wider and shorter muzzle and greater mastoid breadth (Stuart and Lister, 2011). Based on ancient DNA evidence, it has been suggested that *P. spelaea* represents a sister clade to modern lion (Barnett *et al*., 2009).

From stable isotopic analysis of cave lion remains from pre-LGM sites in the Swabian Jura, Germany and Belgian Ardennes, Bocherens et al. (2011) found that prey choice of cave lion did not overlap with that of contemporary predators (*U. arctos, C. crocuta*, and *C. lupus*), and instead relied heavily on reindeer and bear cubs. The study also found no isotopic evidence that cave lions hunted juvenile mammoth (Bocherens *et al*., 2011).

The isotopic signatures therefore indicated no prey overlap between cave lion and hyaena, implying competitive exclusion between them (Bocherens *et al*., 2011). The apparent more solitary behaviour of cave lion may also have been the reason for reduced competitive interaction with *C. lupus* (Bocherens *et al*., 2011).

In the specific case of the Bocherens et al. study from two European upland areas, which by no means can be used as an overall proxy for lion/wolf interaction, cave lion apparently outcompeted wolf for access to reindeer, since this species is a typical prey item for high latitude wolves at the present day. This would in turn force wolf towards other resources, such as horse, giant deer, bison or hare, for which it would compete with brown bear and spotted hyaena.

H. latidens may have been periodically present in the Late Pleistocene, albeit very cryptically. Proctor et al. (2005) reported its possible presence from the Cave Earth deposits at Kents Cavern and at Robin Hood's Cave at Creswell Crags (McFarlane and Lundberg, 2013)**.** *Homotherium* would have been smaller than the large Late Pleistocene lions (*P. leo* and/or *P. spelaea*) but was potentially more gracile, operating as a cursorial and social predator (Anton *et al*., 2005). It is not known whether the taxon survived cryptically throughout the Middle and much of the Late Pleistocene or whether the sabre-toothed cats apparently present during the Middle Devensian in Britain represent a re-immigration from North America. Certainly, the reduction in large carnivore diversity during the Late

Pleistocene in Europe may have liberated ecological niches that would have facilitated its re-establishment.

As with MIS 7, during which Neanderthals were present, MIS 3 also contains evidence of abundant *Homo neandertalensis* from sites such as Lynford, Pin Hole Cave and Kents Cavern. However, Neanderthals gradually disappeared from Britain after 41-42 Ka BP (White and Petitt, 2012a), and from Europe between 40-30 Ka BP (Bocquet-Appel and Demars, 2000) with their latest survival known from Gorham's Cave, Gibraltar at c. 28 Kyr BP (Finlayson *et al*., 2006).

The disappearance of Neanderthals has been associated with the dispersal of *Homo sapiens* into Europe c 42-43 Ka BP, with the change from Neanderthal Mousterian and transitional industries to the early Aurignacian techno-complex highlighting this dispersal (Higham *et al*., 2011). Artefacts of the Aurignacian represent the first unequivocal evidence of *H. sapiens* in Europe, which in Britain are from Kents Cavern, Paviland and Ffynon Beuno Cave (White and Petitt, 2012a). However, skeletal evidence of *H. sapiens* during the earliest part of this period is rare.

Higham et al. (2011) reported that a human maxillary fragment from Kents Cavern represented the oldest dated modern human remains in northwest Europe, with a radiocarbon date estimate 44.2-41.5 Ka cal. BP placing anatomically modern humans as directly contemporary with some of the latest European Neanderthals (Higham *et al*., 2011). However, this dating estimate was considered controversial by White and Petitt (2012b) on numerous accounts, namely that the age estimate was not a 'direct date' from the maxilla, but established though Bayesian modelling of ultrafiltrated AMS dates from fauna excavated during the same period below the fragment. The maxillary fragment was also recovered during a poorly executed excavation in 1927 and there is a pronounced lack of spatial correlation between the specimen and the modern human Aurignacian artefacts at the site (White and Petitt, 2012b). Thus, the arrival of *H. sapiens* is controversial in terms of its timing.

Based on carbon and oxygen stable isotopic analysis by Richards and Trinkaus (2009), early modern humans present between 40-27 Ka in Europe had more varied diets than Neanderthals. However, there is some evidence for Neanderthal dietary flexibility from the Mediterranean and near East with the inclusion of marine shell fish and tortoises, as well as hare and rabbit (Stiner *et al*., 1999). For modern humans, the wide ranging isotopic values indicated that dietary protein came primarily from herbivores, as well as highlighting

evidence of fresh water and marine resource utilisation (Richards and Trinkaus, 2009). Thus, although modern humans may have had more dietary flexibility than Neanderthals, they likely hunted similar herbivorous prey. In regions where they overlapped, competition for prey would have been high. Hunting herbivorous prey would have brought both human species into competition with the large carnivores present.

In summary, as during MIS 7, the large carnivores present during MIS 3 likely exerted similar competitive pressure on *C. lupus*. However, by being able to incorporate non-flesh foods into its diet, facilitated by the overall warmer nature of MIS 3 and greater range of resources, *C. lupus* was able to maintain flexibility.

In contrast to the evidence from MIS 5a, the large carnivores constrained the body size and diet of *C. lupus*, and the carnivorous adaptations specific to MIS 5a were apparently absent during the more diverse and favourable environment of MIS 3. From the lack of severe tooth wear, carcasses were not as fully and rapidly consumed as in MIS 5a, perhaps indicating that prey was more abundant and inter- and intraspecific competition was reduced.

Modern *C. lupus* has a large body mass range of 18-80Kg (Mech, 1974), which encompasses all the estimates for Pleistocene *C. lupus* but with a mean weight exceeding that of Pleistocene wolves (41.33Kg, compiled from various sources see Table 5.17). The diet of modern *C. lupus* is well established in North America (Voigt *et al*., 1976; Fritts and Mech, 1981; Paquet, 1992; Boyd *et al*., 1994) and Europe (Jędrzejewski *et al*., 2000; Kojola *et al*., 2004; Capitani *et al*., 2003; Ansorge *et al*., 2006; Nowak *et al*., 2011). The wolf hunts a wide range of prey, with successful capture of the largest size herbivores (e.g. elk) aided by its cooperative hunting behaviour. It has a varied diet, including high proportions of both flesh and non-flesh food, which correlates well with the results from the analysis of cranio-dental variables here. Modern Swedish wolves were found to have strong, deep jaws and an increased ability to slice flesh, exceeding that seen in MIS 3 and 7 wolves, as well as an increased ability to crush non-flesh foods. Some minor ability to crack bone existed in the population studied here, although not to the same extent as in MIS 5a.

In comparison to the long chronological ranges of the Pleistocene species, the modern carnivore community in Europe has drastically changed over a very short period of time. *P. leo* and *C. crocuta* are now locally extinct in Europe and are both restricted to sub Saharan Africa, with the exception of a small remnant population of lion in the Gir Forest of northern India (Bauer *et al*., 2012).

In Sweden, where the analysed modern wolf population originated, *U. arctos* is present with a population of 800-1,300 estimated in spring 1996 (Swenson *et al*., 1999), with regionally 223 (188-282) bears present in south central Sweden (area of 7328 km^2) during 2001-2002 (Flagstad *et al*., 2003) where the majority of the modern analysed population were from. In comparison, wolf numbers were much lower, with estimates from Sweden and Norway combined during 1997-1998 of only 50-72 wolves present, comprising 6 packs over an 86,000km^2 area (Wabakken *et al*., 2001).

In terms of population density, bears were represented in northern Sweden by 1.2 ±0.81 adult females per 1000Km^2, and 1.06 ±3.44 adult females per 1000km^2 in the south during 1991 (Swenson *et al*., 1994). More recently, similarly low densities were estimated for wolves across Sweden and Norway at 1/1000km^2, although noticeably increasing within wolf territories up to 10/1000km^2 (Wabakken *et al*., 2001). Hence, unless bears were within wolf territories, both species were of low density and interactions would be limited.

Although modern brown bears are omnivorous, with plant material and berries an important component of their diet, carrion is often consumed including Eurasian elk, reindeer, red deer and bison, as well as the hunting of weak or old ungulates (Pasitschniak-Arts, 1993). Thus, wolf kills could potentially be scavenged and some competition over ungulate prey is possible, although perhaps a more seasonal occurrence due to the highly flexible diet of bears.

Lynx are also present in Sweden and although recent population estimates are lacking, their population in Scandinavia is increasing from an earlier 20th century bottleneck (Rueness *et al*., 2003a). Lynx are solitary ambush predators, each exploiting very large home ranges (Rueness *et al*., 2003a), estimated as 600-1400 km^2 for males and 300-800km^2 females (Linnel *et al.,* 2001) and hence population densities may be low as a result. The main prey of lynx in Norway and Sweden is roe deer and (semi-domesticated) reindeer, although it also includes mountain hare, capercaille, black grouse as well as domestic sheep (Linnel *et al*., 2001), with the large prey choices of lynx overlapping with wolves.

The wolverine population in Sweden is estimated at 780 individuals occurring at low population densities (Persson *et al*., 2009). Wolverines weigh up to 25Kg, and are both scavengers and hunters, often capturing prey much larger than themselves (Macdonald, 2009). In Scandinavia, reindeer is their main prey (Landa *et al*. 1997; Persson *et al*., 2009), with domesticated sheep and hares also hunted and small rodents an important source of food for wolverine cubs (Landa *et al*., 1997). In areas where wolves and wolverines coexist,

the increase in the availability of large prey carcasses, such as *A. alces* from wolf kills, increases scavenging in wolverines, with their diet shifting to include more Eurasian elk and less reindeer, and more small prey in comparison to areas without wolves (Dijk *et al*., 2008). Hence, where wolves and wolverines overlap in their ranges, wolves provide an important food source for wolverine, although scavenging from wolf kills is not without risk.

As discussed in section 6.1, the reduction in body size in Swedish wolves at latitudes >60°N may be related to competition, as well as lower resources in sub-Arctic regions. At high latitudes, *U. arctos* may be more in competition with *C. lupus* than at lower latitudes. A study from the Pasvik Valley, northeastern Norway (69°N), demonstrated that comparatively high percentages (up to 85%) of bear diet consisted of Eurasian elk and reindeer, as a consequence of ease of predation and lack of alternative resources (Persson *et al*., 2001). Inland Sweden has no visiting polar bears (*Ursus maritimus*): the species' extent in northern Europe is limited to the Barents Sea including Svalbard and Franz Josef Land, as well as high latitude North European Russia (west of the Urals) (Schliebe *et al*., 2008). Lynx are also present at high latitudes (67°N) (Linnel *et al.*, 2001), with similar prey preferences of reindeer, as well as roe deer.

The carnivore community represented in Sweden, namely bear, lynx, wolf (and wolverine, although their range is more restricted to high latitudes [Macdonald, 2009]), is slowly returning to Europe (Trouwborst, 2010), with the three large carnivores also present in the Alps (Breitnmoser, 1998), Poland and Belarus (Jedrzejewski et al., 1996). In North America, wolves inhabit Canada and Alaska, as well as northern states including parts of Montana, Idaho and Wyoming, Minnesota and Wisconsin (Mech and Boitani, 2010). The large members of the carnivore community of these areas is also comprised of brown bears and grizzly bears (*Ursus arctos*) (west and northern Canada, Alaska, parts of Montana, Idaho and Wyoming, and Washington state [McLellan *et al*., 2008]), Canadian lynx (*Lynx Canadensis*) (northern North America [Rueness *et al*., 2003b]), mountain lion (*Puma concolor*) (western Canada and west and central USA [Caso *et al*., 2013]) and coyotes (*Canis latrans*) (throughout North America [Gese *et al.*, 2008]).

From studies of mountain lion and wolf prey selection in Montana, both carnivores were found to prefer white tailed deer (*Odocoileus virginianus*), although wolves also predated North American elk (*Cervus canadensis*) and moose (*Alces alces*), thereby increasing their

available prey base (Kunkel *et al*., 1999). Thus differential prey use and abundant other prey in the area resulted in low competition between the predators (Kunkel *et al*., 1999).

Similarly, from studies in Riding National Park, Manitoba, where wolves and coyotes overlap, differential use of resources minimises competition, as although both canids selectively hunted red deer and white tailed deer, coyotes tended to scavenge from wolf kills, and supplement their diet with smaller prey (Paquet, 1992) indicating some slight prey differentiation.

There have also been numerous studies on the positive effect reintroduction of wolves has had on ecosystems, such as at Yellowstone National Park. Wolves were reintroduced in 1995 to promote recovery of the endangered wolf in the Rocky Mountains and restore the park to its former, more biodiverse state (wolves were regionally extirpated by mid-20th century in Yellowstone) (U.S. Fish and Wildlife Service, 1987).

Although the full effect of wolf reintroduction will not be evident for decades (Smith *et al*., 2003), the presence of top carnivores is integral in maintaining biodiversity, with reintroduced wolves controlling the ungulate community, creating increased food for scavengers through ungulate predation (Smith *et al*., 2003). Wolf reintroduction at Yellowstone also has had an indirect effect on quaking aspen (*Populus tremloides*) recovery, whereby the presence of wolves has controlled elk browsing and movement patterns, enabling regeneration of aspen, with concomitant benefits for the rest of the vegetation (Ripple *et al*., 2001; Fortin *et al*., 2005).

The most competition for wolves comes from humans. Human-carnivore conflict is caused by shared reliance on a protein-rich diet, and overlapping home ranges (Treves and Karanth, 2003). Scarcity of wild ungulates, presumably either naturally or because of anthropogenic impacts, can also increase predation by wolves on domestic livestock (Meriggi and Lovari, 1996), and, albeit rarely, human-carnivore interaction can result in death (for both parties) and vilification (for the carnivore).

In terms of wolf attacks, in Wisconsin between 1976-2002, there were 121 verified wolf related incidents including attacks on livestock (cattle, sheep, horse) 42%, farmed deer 4%, and pet dogs 48% (Treves *et al*., 2002; Naughton-Treves *et al*., 2003). Attacks on humans are much rarer, especially from the 20th Century with 45 children killed in Poland, Spain and Russia from 1937-1974 (Linnel *et al*., 2002). In North America, no deaths were recorded in the 20th Century, although 8 documented attacks have occurred (Linnel *et al*., 2002).

In summary, modern *C. lupus* is less constrained in terms of its body size (mean 41.33Kg, e.g. range 18-80Kg [Mech, 1974]) due to the lack of large carnivore competitors, which may partly explain some of the shared features between modern and MIS 5a wolves. Competition is primarily from humans, who exert considerable pressure on populations, particular those close to human settlements.

The diet of modern European *C. lupus* is ostensibly more flexible than at many times during the Pleistocene, since cranio-dental measurements indicate an ability both to slice flesh quickly and to crush non-flesh foods, leading to a broader range of available resources. The increased ability to hunt large prey up to 800Kg for Eurasian elk (Macdonald, 2009) also suggests that reduced competition from other carnivores has further enhanced feeding opportunities for modern populations.

6.3.1.4. Summary

Predator body size limits the size of prey a carnivore can tackle alone, as well as the ability to chase, seize and kill. Based on the 21.5Kg dietary threshold, large predators can exploit both smaller and larger prey, whereas smaller predators are restricted to small prey only. However, this is overruled by cooperative hunting enabling predators to hunt much larger prey than their individual body size would suggest.

Although both large enough to hunt prey greater than themselves, *C. etruscus* and *C. mosbachensis* were apparently constrained in body size by the predominance and diversity of larger carnivores in the Early to Middle Pleistocene. For *C. etruscus* in particular, relatively stable and productive climatic and environmental conditions supported abundant and diverse prey, which in turn sustained a rich carnivore guild. The differences in carnivore body sizes and predation strategies aided resource partitioning amongst the members of the guild (Anton *et al*., 2005).

By the Late Pleistocene, changes in carnivore community structure and dramatic fluctuations in climate, environment and palaeogeography required flexible responses on the part of wolves. *C. lupus* became less constrained in body size, partly perhaps because of a Bergmannian response to climatic deterioration but also because of the reduction in large carnivore competitors. Wolves were also very successful because of their exceptional adaptability and dietary flexibility. This is particularly highlighted by the evidence from MIS 5a, where *C. lupus* was able to cope with exceptionally severe environmental conditions,

low resource availability, nutritional stress and high competition. This exceptional adaptability is equally evident in modern *C. lupus*, with high levels of anthropogenic competition and persecution the most limiting factors on their ecology and distribution.

6.4. Inferences on the wolf lineage

C. etruscus, *C. mosbachensis* and *C. lupus* are together widely considered to form an evolutionary lineage of wolf-like canids (Torre, 1979; Rook and Torre, 1996b; Sotnikova, 2001; see Chapter 2), on the premise that *C. etruscus* evolved into *C. mosbachensis*, before increasing in size and becoming *C. lupus* during the Middle Pleistocene.

However, the phylogenetic position of *C. mosbachensis* regarding its status as a separate species in its own right, or a subspecies of *C. lupus*, is much debated. Accordingly, some authors have described it as *Canis lupus mosbachensis* (Thenius, 1954; Kurtén, 1968; Kurtén and Poulianos 1977, 1981; Lumley *et al*., 1988; Argant, 2009) to reflect its close affinity with *C. lupus*.

Alternatively, *C. mosbachensis* was found to have no clear anatomical relationship with either *C. etruscus* or *C. lupus* by Martinez-Navarro et al. (2009), and based on size and dental morphology, it was deemed to be more closely related to extant jackals. Further to this, *C. mosbachensis* is thought to have had a closer phylogenetic relationship with *C. arnensis* than with *C. etruscus* (Soergel, 1928; Thenius, 1954; Kurtén and Poulianos, 1977; Garrido and Arribas 2008). It was accordingly excluded by these authors from the wolf lineage and reassigned to the coyote lineage of *C. arnensis* (as proposed by Kurtén [1974]). This study therefore offers an opportunity to re-examine the integrity of the wolf lineage, as well as to discuss the relationship between *C. mosbachensis* and *C. lupus*.

6.4.1. Morphological differences

The present study has identified numerous shared features between the different canids analysed (see Chapter 2), such as accessory cusps on the p4 apparent in *C. etruscus* and *C. mosbachensis*, the comparable m1 paraconid height in *C. etruscus* and *C. arnensis*, and the m1 talonid cusp morphology common to *C. etruscus, C. mosbachensis* and *C. lupus*.

In a study comparing cranial measurement ratios, Cherin et al. (2013a) found that *C. arnensis* shared some similarities with *C. lupus* in terms of cranial morphology, specifically in the ratio of molar row length to cheek-tooth row length, as well as viscerocranium length to total cranium length. Interestingly, these measurement ratios are apparently more similar than between even *C. etruscus* and *C. lupus*, with *C. etruscus* having unique features separate from either canid, such as the ratio of viscerocranium length over total cranium length, breadth of occipital condyles to height of occipital triangle, as well as longer nasals

relative to total cranium length (Cherin *et al*., 2013a). The authors accordingly stated that the use of 'wolf-like' and 'jackal-like' as terms of reference were an oversimplification, based on the cranial characteristics examined.

In terms of dentition, *C. etruscus* was found in the present research to share similarities with *C. mosbachensis*, such as a lower positioned p3 in the mandible in comparison to the adjacent p2 and p4, the presence of a small secondary accessory cusplet positioned in front of the posterior cingulum, as well as a pronounced anterior buccal cingulum below the paraconid on the m2 (see Chapter 2).

To a lesser degree, some of these characters were also noted here in *C. arnensis*, although they are not a constant feature and are not pronounced, and may reflect normal variation within this species. Hence, the presence of shared dental morphology suggests that *C. etruscus* and *C. mosbachensis* have a phylogenetic affinity.

One of the features separating *C. arnensis* from the other canids was the wide diastema present between the upper premolars (see Chapter 2). However, it was noted by Garrido and Arribas (2008) that *C. arnensis* was characterised by a distinct lack of diagnostic features, and that many of its cranio-dental characteristics were related to intraspecific variation, as considered in this present research. Furthermore, the authors thought that the differentiation of *C. arnensis* was largely based on metric data, and that the specific diagnosis of the taxon needed to be re-established in light of more clear-cut characteristics that are not as common throughout the genus *Canis* (Garrido and Arribas, 2008).

In the present research, a much higher degree of similarity was found between *C. etruscus* and *C. mosbachensis*, rather than between *C. mosbachensis* and *C. arnensis*. Thus, there is less clear evidence for an *arnensis-mosbachensis* link and an *etruscus-mosbachensis* relationship is more readily apparent.

In general, *C. lupus* had much larger and broader cranio-dental morphology compared to the other canids (see Chapter 2) although some similarities were present with *C. etruscus* and *C. mosbachensis* in the dentition that were not found in *C. arnensis*, for example the more complex m1 talonid ridge morphology. Although these features were highly variable in the *C. lupus* specimens examined, the presence of a transverse cristid from the hypoconid to entoconid, an oblique cristid from the hypoconid, and a crest between entoconid and metaconid were all observed, if not together on a specimen, then separately.

However, as mentioned previously, similarities were found between *C. lupus* and *C. arnensis* based on ratios of cranial measurements by Cherin et al. (2013a), suggesting some shared features on the basis of size between the two canids. The larger overall size of the *C. lupus* material has accordingly been used as an important distinguishing feature for its presence (Turner, 2009; Sotnikova 2001), particularly from MIS 7 onwards.

6.4.2. Alternative ancestors and 'likeness'

The classification of 'wolf-like' for *C. etruscus* and 'coyote-like' for *C. arnensis* was traditionally based on mandibular characteristics. However, as mentioned, this was considered as too simplistic by Cherin et al. (2013a) since, for example, *C. arnensis* shared characteristics with *C. lupus* and *C. etruscus* had features unique to it alone, as described in the previous section. The shared morphological features found in the present research between *C. etruscus, C. arnensis, C. mosbachensis* and *C. lupus* as described above echo this view. The attribution of the 'likeness' of an extinct species to a modern species (e.g. 'wolf-like') is commonplace, placing the 'unknown' animal into a modern ecological context. However, if these classifications are indeed overly simplistic, the use of a modern frame of reference is potentially misleading and an extinct species should, in preference, be considered in its own right.

It is worth noting that Kurtén and Poulianos (1977) suggested that *C. arnensis* might actually be the ancestor of *C. lupus*. As *C. arnensis* is considered to be closely related to coyotes (after Kurtén, 1974), these authors thought that hybridisation between modern coyotes and wolves in North America was indicative of a close relationship between the canids. Furthermore, from recent analysis of coyote mtDNA from northeastern USA, Kays et al. (2010) found hybridisation of these coyotes with wolf DNA local to the Great Lakes region in Canada. This hybridisation introduced genetic variation in terms of promoting cranio-dental adaptations in coyotes for capturing large prey, such as increased areas for masticatory musculature more similar to wolves. However it was noted that this particular hybridisation event was a relatively recent occurrence and that the morphological response to the introgressed wolf DNA had not had sufficient time to fully develop (Kays *et al*., 2010).

The possible link between *C. arnensis* and *C. lupus* was also echoed by the identification of shared features posited by Cherin et al. (2013a). However, the differences found between *C. arnensis* and *C. lupus* in the present study are much higher and are more consistent with *C. etruscus* as the ancestor of the modern wolf.

As discussed in Section 6.2, the discriminant analysis of species groups found that *C. etruscus, C. mosbachensis* and *C. arnensis* grouped more closely together than with *C. lupus*, and within this group, *C. etruscus* was both most separated from *C. arnensis* and relatively the closest to *C. lupus* on the most explanatory function (explaining 86.2% variation). This would support a close relationship between the earlier Pleistocene canids and uphold a comparatively close relationship between *C. etruscus* and *C. lupus*. In terms of dietary indicators, *C. etruscus* was also found to be the most similar to *C. lupus*.

When modern canids were included in the species DFA, it is interesting to note that the jackals (*C. aureus, C. adustus* and *C. mesomelas*) plotted closely together and were clearly separated from all other canids on the most explanatory function. The jackals were included on the basis that *C. arnensis* was originally considered to be related first to jackals (Kurtén, 1968) and then later, to coyotes (Kurtén, 1974). *C. mosbachensis* was also thought to be similar to jackals (Martinez-Navarro *et al.*, 2009).

The results indicated that on the first function, both *C. arnensis* and *C. mosbachensis* plotted away from the jackal group and grouped most closely with *C. alpinus* and *L. pictus*, particularly in terms of m1Ltrig and m1W (differences in m1 talonid length, which may reflect the hypercarnivorous adaptation of these canids, were not selected by the step-wise model). However, the second function (explaining 9.6% of the variation) implied more of a relationship between *C. arnensis*, C*. mosbachensis* and the jackals, in terms of molar crushing capacity and comparability, in particular, with *C. adustus*. Thus, some similarities between the two Pleistocene species and the jackal group exist, although they are not the dominant characters.

Similarly, a PCA carried out by Cherin et al. (2013a) plotted the jackals *C. aureus, C. mesomelas* as well as *Canis lupaster* together as one group, with *C. arnensis, C. etruscus* and *C. lupus* clustering as a separate group. Although *C. mosbachensis* was not analysed in their study, it is revealing that a comparable low affinity with jackals was found amongst the other Pleistocene species.

As previously discussed in section 6.2, *C. mosbachensis* plotted between *C. etruscus* and *C. arnensis* on the species DFA, rather than plotting closer to *C. lupus*, as would perhaps be expected considering the assumed order of the species in the wolf lineage. Ultimately, this position reveals the conflict over whether *C. mosbachensis* was more related to *C. arnensis* or to *C. etruscus*, since in terms of the most explanatory discriminant function, it lies between both species.

However, the dietary analyses revealed that *C. mosbachensis* was more carnivorous than either *C. etruscus* or *C. arnensis*, and on the most explanatory function, it was clustered separately with *L. pictus*. Although it is not suggested that *C. mosbachensis* was as hypercarnivorously-adapted as the modern wild dog (based on its molar crushing abilities from function 2, as well as overall molar morphology), it is interesting to note this proximity.

Sardella and Palombo (2007) suggested that *C. mosbachensis* partially occupied the niche of '*Lycaon*' (= *C.* (*X.*) *lycaonoides*). As discussed in Section 6.3, in terms of prey size choices based on body size and inferred overlap, competition would potentially have occurred between both *C. etruscus* and *C. falconeri*, as well as between *C. mosbachensis* and *C.* (*X.*) *lycaonoides*.

Both *C. mosbachensis* and *C.* (*X.*) *lycanoides* may have been ecological replacements for *C. etruscus* and *C. falconeri*. However, *C.* (*X.*) *lycaonoides* was perhaps more carnivorous than its possible predecessor, based on its closer morphological similarity to modern *L. pictus*. This shift towards hypercarnivory in *C.* (*X.*) *lycaonoides* may have enabled *C. mosbachensis* also to increase its degree of flesh consumption, as a knock-on effect of niche changes in *C.* (*X.*) *lycaonoides* and higher up in the carnivore community, and thus become relatively more carnivorous than *C. etruscus*.

6.4.3. The presence of two late Early-early Middle Pleistocene canid lineages

As introduced in Chapter 2, Rook and Torre (1996b) proposed that the Early to Middle Pleistocene of Europe contained two canid lineages, one with the less-derived Early Pleistocene *C. arnensis*, which became *C*. aff. *arnensis* (advanced form) and occupied the Mediterranean region, and the other containing the Early Pleistocene *C. etruscus*, which became *C. mosbachensis*, and occupied a more northerly region, in central and northern Eurasia.

Evidence of the advanced form *C*. aff. *arnensis* was accordingly recognised by Rook and Torre (1996b) at the French sites of Le Vallonet and l'Escale, Colle Curti and the Soave sites including Castello, Zoppega and Viatelle in Italy, and Petralona in Greece. According to the authors, combined with the palaeogeographical differences, the northern *C. mosbachensis* can be differentiated from the southern *C*. aff. *arnensis* by its larger size, which is more comparable to *C. etruscus*.

The material attributed to *C. mosbachensis* in this research is from both northern Europe (Britain and Germany) and southern Europe (Italy). Thus, in order to explore whether size differences were present between these canids, which might identify both the larger northern form of *C. mosbachensis* and the smaller southern form of *C*. aff. *arnensis* proposed by Rook and Torre (1996b), m1L was compared including published measurement values from Petralona and l'Escale given by Kurtén and Poulianos (1977).

The comparative graph (Chapter 5, section 5.1.7, Figure 5.60) illustrates the trend of the northern members of *C. mosbachensis* (Grays Thurrock, Heppenloch, Sidestrand, Westbury, Untermassfeld), which were more comparable in size to *C. etruscus* (from Olivola and Upper Valdarno), as well as the southern members of *C*. aff. *arnensis* (Petralona, l'Escale, Monte Zoppega) being comparably smaller in size (as noted by Kurtén and Poulianos (1977).

In a more recent study, Baryshnikov and Tsoukala (2010) also compared the lower carnassials of the Petralona *C*. aff. *arnensis* to *C. mosbachensis* from Westbury-sub-Mendip, noting that the Westbury specimens were larger, although with some overlap in variation. Based on the comparison of m1L (Chapter 5, section 5.1.7, Figure 5.60) undertaken here, the Petralona and Westbury specimens (based on a much larger group than used by Baryshnikov and Tsoukala [2010]) were also found to overlap in variation, although mean m1L was found to be higher at Westbury.

Thus, the presence of overlapping variability between both sites suggests high variation between both 'species', questioning whether the regional differences in size distinguishing northern *C. mosbachensis* from southern *C*. aff. *arnensis* are simply geographical variation within a single canid species. In support, Garcia and Arsuaga (1999) thought that *C*. aff *arnensis* and *C. mosbachensis* were synonyms, based on the lack of coyote-like morphology akin to *C. arnensis* in specimens attributed to the southern European more advanced *C*. aff. *arnensis.* They attributed both *C*. aff. *arnensis* and *C*. *mosbachensis* to a single 'small wolf' species.

Further to this, a much closer association was found between the Petralona *C*. aff. *arnensis* and Boxgrove *C. mosbachensis* material, which was also found to be similar to the l'Escale *C*. aff. *arnensis* specimens. The fact that a northern European locality (which supposedly contains only the larger, northern *C. mosbachensis* according to Rook and Torre's [1996b] two lineage theory) has yielded a canid of a similar size to the smaller southern European *C*. aff. *arnensis* is interesting.

However, It seems very unlikely that the smaller, southern *C*. aff. *arnensis* migrated north to Britain, especially since the individual from Sidestrand (of similar age to Boxgrove) was more similar to the larger 'northern lineage'. If the smaller Boxgrove *C*. aff. *arnensis* were indeed sympatric with the larger northern *C. mosbachensis*, the two species would have been in direct competition, due to both being medium-sized and with overlapping dietary requirements. However, no evidence was found at Boxgrove of increased tooth wear and breakage that would suggest higher levels of competition. It therefore seems more likely that the Boxgrove specimens should also be attributed to *C. mosbachensis* and that there is intraspecific variation in size.

Consequently, it seems less plausible that two apparent canid lineages were present in Europe during the late Early to early Middle Pleistocene. The size difference and the variability between the supposedly northern *C. mosbachensis* and the southern *C*. aff. *arnensis* may therefore represent regional differences within a single species (considered here solely as *C. mosbachensis*), driven by climate as observed in the Bergmannian size cline between modern high latitude *C. lupus* from Sweden and its more southern European counterparts. Thus, regional differences in environmental conditions may impact on morphology but not necessarily lead to speciation, and it is on this basis that caution should be exercised when designating regional populations into separate species and lineages.

6.4.4. Problems with body size in phylogenetic inferences

Another problem with the wolf lineage (as currently understood) is that the line from *C. etruscus* to *C. mosbachensis* to *C. lupus* does not represent a simple increase in size (Rook and Torre, 1996b). Thus, a reversal size trend from the larger *C. etruscus* to the smaller *C. mosbachensis* was noted (Kurtén and Poulianos, 1977), and subsequently used to question the derivation of *C. lupus* from this lineage (Rook and Torre, 1996b).

Based on the body mass estimates calculated here, *C. mosbachensis* was slightly smaller than *C. etruscus* (22.50 ±1.62Kg and 24.34 ±1.65Kg respectively), although overlapping in its body size range. However, it seems unreasonable to sustain the view that a smaller canid could not give rise to a larger descendant, especially if environmental and competitive conditions were much changed between them. Kurtén and Poulianos (1977) equally found this trend not unusual in the Pleistocene carnivore record.

As introduced in Chapter 3, the tendency of animal lineages to evolve towards larger size over time, i.e. that a small progenitor can give rise to a larger successor, is the main thesis of Cope's Rule (Stanley, 1973; Benton, 2002). The validity of the rule relates to the benefits of increasing size and includes increased prey capture success, expanded food range, greater reproductive success and extended longevity (Stanley, 1973; Hone and Benton, 2005). Although evidence for Cope's Rule exists in mammals (Alroy, 1998), and has been invoked to some extent to explain the multiple and independent trends of increasing size in the Canidae over time (Van Valkenburgh *et al*., 2004, FInarelli and Flynn, 2006; Finarelli, 2007), not all animal groups follow this rule (e.g. Jablonski, 1997), and hence recognition of the law is not without controversy.

Nonetheless, Pleistocene tremarctine bears, for example, illustrate well the ability of a smaller ancestor to give rise to a much larger descendant. The ancestral *Plionarctos harroldorum* had an estimated body mass of 84.44kg. This was estimated by the present author, based on a single m1 length published in Tedford and Martin (2001), and using Van Valkenburgh's (1990) predictive regression equation for Ursidae using m1L (%SEE 78, %PE 46), and with QMLE correction factor applied for logarithmic transformation bias. It should be noted that m1L was not considered the best predictor of body mass in ursids (Van Valkenburgh, 1990), and has notably high estimation errors as shown above. This was comparable in size to a modern spectacled bear (*Tremarctos ornatus*: males 100-175Kg, females 60-80Kg [Macdonald, 2009]), its closest living relative (Krause *et al*., 2008). *Plionarctos* gave rise to a much larger descendant, the giant short-faced bear *Arctodus simus* (body mass 613Kg [Christiansen, 1999]), during the Pleistocene.

It is also noteworthy that the increasing size trend is readily reversible, since the modern spectacled bear is much smaller in size again, and consistent with a reduction in size found in numerous mammals during the Late Pleistocene-Holocene (e.g. Davis, 1981; Forstén, 1993), including wolves and foxes in Israel (Davis, 1981), although temperature and latitude are also important factors.

Ultimately, body size should not be a consideration when discussing lineage relationships as it is evolutionarily plastic - fluctuating between larger and smaller, and relating to a wide range of environmental and ecological factors that should not be used for establishing phylogeny.

6.4.5. The presence of chronospecies

The classic wolf lineage of *C. etruscus, C. mosbachensis* and *C. lupus* was also considered as representing three main chronospecies by Brugal and Boudadi-Maligne (2011), implying that only one species was present in the lineage at any point in time.

However, the presence of *C. lupus* at La Polledrara di Cecanibbio, Italy, correlated with MIS 9 (Gliozzi *et al*., 1997) partly questions this assumption. As discussed, although *C. lupus* was not recorded in Britain until MIS 7, *C. mosbachensis* was present during the preceding interglacial, MIS 9. This may suggest that either Britain represented a northern refugia for *C. mosbachensis*, or that *C. lupus* simply took longer to immigrate into Britain, which considering its Eurasian origination would be highly likely.

A number of sites were originally believed to show the presence of both *C. mosbachensis* and *C. lupus* together, such as the late Middle Pleistocene (Middle or Late Galerian) Cerè Cave in Italy (Rook and Torre, 1996b; Zorzin *et al.*, 2003). However, recent analysis by Ghezzo et al. (2013) has reconsidered all the remains as belonging only to *C. mosbachensis*. Similarly, the assemblage from the *terre rosse* of the karst infill at San Sidero, in southern Italy (level 3) was also believed to contain both *C. lupus* and *C. mosbachensis*, in association with *C. alpinus* (Rook and Torre, 1996b; Iurino *et al*., 2013). In this case, the early Late Pleistocene age for the site seems at odds with the presence of *C. mosbachensis* and it is more likely that this represents a mixed assemblage (Iurino *et al*., 2013).

On balance, at present, evidence of regional overlap is scarce and not without problems in interpretation. However, the extended record of *C. mosbachensis* in Britain is potentially of note, and would benefit from investigation of other MIS 9 northern European sites if their chronological attributions were to be refined.

6.4.6. Variability in *Canis lupus* and its relationship with phylogeny

Pleistocene *C. lupus* was larger than *C. etruscus, C. arnensis* and *C. mosbachensis*, with body mass estimated as 35.81 ±1.59Kg (for Britain: 36.25 ±1.59Kg, for mainland Europe: 34.23 ±1.64Kg). Its multi-specialisation in diet in terms of flesh slicing, crushing of non-flesh foods, strong jaws and the ability to crack and crush bone, enabled a high level of flexibility, allowing *C. lupus* to incorporate a wide range of foods into its diet. This sits well with modern *C. lupus* being a hypercarnivore, albeit one with a generalist diet as shown by its retention of post carnassial molars and a bicuspid m1 talonid.

The dietary spectrum of *C. lupus* is reminiscent of both *C. etruscus* and *C. mosbachensis*. It therefore seems reasonable that with the significant decrease in carnivore diversity during the Middle Pleistocene, *C. lupus* was less constrained by competitors, especially larger canids. Combined with the availability of large prey and open grassland environments, *C. lupus* was able to enlarge its predatory niche and increase in size in comparison to the earlier canids.

However, in contrast to the earlier taxa, which showed relative dietary stability, both the body mass and diets of Pleistocene *C. lupus* showed variation, with MIS 5a *C. lupus* estimated as larger (39.85 ±1.64Kg) than both MIS 3 and 7 wolves, which were themselves similar at 34.03 ±1.73Kg and 35.40 ±1.63Kg, as well being larger than other age groups.

The similar size of MIS 3 and 7 *C. lupus* correlated with their comparable diets. Wolves from both periods were more adapted to non-flesh food crushing and less adapted to fast flesh slicing, combined with possessing comparatively weaker jaws than their MIS 5a and modern counterparts. Thus the wolves from MIS 3 and 7 were hunters of prey larger than themselves, aided by cooperative hunting. It is suggested here that they were perhaps less likely to target prey as large as modern wolves on account of their slightly smaller size and increased levels of carnivore competition during these stages.

In contrast, the larger MIS 5a *C. lupus* was better adapted for fast flesh slicing than non-flesh food crushing, combined with increased bone cracking ability and broader jaws for manipulating large prey. The significant differences in MIS 5a *C. lupus* were related to climate, environment, isolation, low prey diversity and competition.

As discussed in section 6.1, the presence of a putative sub-species *Canis lupus maximus* at Jaurens Cave in southern France, correlated with late MIS 3, was found to be significantly larger in size than *C. lupus* from France, as well as extant wolves from southern Europe based on m1L (Boudadi-Maligne, 2012). This subspecies was not identified in Britain in MIS 3 during the present study. Apart from differences in size, the author also noted other distinguishing features of the subspecies as having more robust teeth, including highly developed posterior cusps (denticules) on the premolars (p2-p4, P2-P3), as well as the mesiodistal diameter of the m1 being significantly different from the other wolves analysed.

However, the large size and association with cold-climate fauna were arguably more reminiscent of the MIS 5a *C. lupus*, including the presence of heavy tooth wear recorded

(although attributed to ontogenetic age) by Boudadi-Maligne (2012). Nonetheless palaeoenvironmental conditions, diversity and competition were markedly different from MIS 3.

The identification of this subspecies by Boudadi-Maligne (2012) however brings into question the appropriateness of differentiating a species primarily on the basis of size. The diagnostic dental morphology given is by no means unusual and within the range of variation found in *C. lupus* in the present study, more likely representing intraspecific variation. Although *C. lupus* from MIS 5a is significantly different from wolves of other climatic stages, it is not considered sufficient differentiation to warrant designation of a sub-species here. Rather, in view of the exceptional flexibility of these animals, it seems more likely that MIS 5a wolves were a specialised group responding to unique environmental conditions.

In contrast, the wolves of MIS 5a may share some similarities with Late Pleistocene *C. lupus* from eastern Beringia. In a study by Leonard et al. (2007), east Beringian *C. lupus* was found to be a specialised hunter and scavenger of Late Pleistocene megafauna on the basis of having shorter and broader palates with large carnassials relative to skull size, as well as shorter and broader rostra combined with deep jaws, all of which enabled relatively large bite forces, and made them uniquely adapted to their environment.

These eastern Beringian wolves were found to differ from both Late Pleistocene coeval Rancho La Brea *C. lupus* and from modern Alaskan *C. lupus* and represented a specialised hypercarnivorous wolf ecomorph, with a diagnostic cranio-dental morphology enabling the capturing, dismembering and full consumption (including bones) of very large mega-herbivores such as bison. Thus, when the mega-herbivores disappeared, so did the wolf ecomorph (Leonard *et al*., 2007).

The form encountered during MIS 5a had disappeared by MIS 3, whereupon *C. lupus* reverted to a similar state to that last seen in MIS 7, based on their shared environmental conditions and constraints. *C. lupus* was highly adaptable in the face of environmental changes, and thus the degree of intraspecific variability observed is considered to be a function of this flexibility.

The modern Swedish wolves were also found to have significant differences in diet compared to the Pleistocene age groups, based on molar crushing abilities and jaw depth. Again, this variation was likely related to environmental and competitive differences.

Modern wolves were also on average larger in size, although range of body mass is large (mean 41.33Kg, range 18-80Kg [Mech, 1974]). Hence, the Pleistocene estimates are all within the large size range of modern *C. lupus*, as were all the other analysed canids based on this size range.

The range of body size observed, combined with the generalist diet, is again characteristic of the Pleistocene flexibility inherited by modern *C. lupus* and part of the normal variation inherent within the species.

6.4.7. *Canis mosbachensis*: the subspecies?

As discussed, *C. mosbachensis* has been identified as a subspecies of *C. lupus* by some authors (Thenius, 1954; Kurtén, 1968; Kurtén and Poulianos 1977, 1981; Lumley *et al*., 1988; Argant, 2009) based on their shared characteristics and assumed close relationship. However, although *C. mosbachensis* does indeed share some morphological features with *C. lupus*, it equally has similarities with *C. etruscus*. Hence, assignation of *mosbachensis* to subspecies level cannot be supported at this point.

In contrast to *C. mosbachensis* and *C. etruscus*, significant differences were found in all cranio-dental measurements analysed here between *C. mosbachensis* and *C. lupus*, more so than between the temporal variants of *C. lupus* itself (for example MIS 5a *C. lupus*). As *C. etruscus* and *C. mosbachensis* were found to be statistically more similar (as were *C. arnensis* and *C. mosbachensis*), it suggests that *C. mosbachensis* perhaps had a closer phylogenetic relationship with both the earlier Pleistocene canids than with later *C. lupus*. The large difference in size between *C. mosbachensis* and *C. lupus*, in comparison to the closer sizes of *C. etruscus, C. arnensis* and *C. mosbachensis*, is also important in differentiating *C. mosbachensis* ecologically from *C. lupus*.

In summary, the present study would uphold the view that *C. mosbachensis* should remain a separate species, rather than a subspecies of *C. lupus*. From the analysis of diet and morphology, *C. etruscus* and *C. mosbachensis* seem most similar, although likenesses between *C. mosbachensis* and *C. arnensis* were also found. Nonetheless, significant differences were found in all cranio-dental measurements taken between *C. lupus* and these early Pleistocene canids, implying less similarity, and hence perhaps less of a relationship.

6.4.8. Other origins and an alternative wolf lineage

The currently accepted understanding of the wolf lineage proposes that *C. mosbachensis* increased in size to become *C. lupus*. Unfortunately abundant Middle Pleistocene material of *C. mosbachensis* in Britain is rare and comparative European mainland sites frequently unresolved in terms of chronology. Overall, there seems to be little strong evidence for a gradual size increase in *C. mosbachensis*. Related to this may be the remark that *C. lupus* was considered to have had an abrupt arrival in Europe (Rook and Torre, 1996b).

The possibility remains that *C. lupus* may not have directly evolved from *C. mosbachensis* in Europe, and is thus distinct from the European *C. etruscus – C. mosbachensis* lineage. The modern wolf would therefore have dispersed rapidly into Europe from Eurasia during the Middle Pleistocene (Rook and Torre, 1996b).

Brugal and Boudadi-Maligne (2011) also considered that the true wolf lineage was potentially separate from the *C. etruscus - C. mosbachensis* lineage. They proposed that the late Middle Pleistocene *Canis lupus lunellensis* represented the first appearance of true wolf, albeit smaller in size, and was the starting point in the development of a western European wolf lineage that subsequently underwent size and morphological changes, represented by the chrono-subspecies of *lunellensis, saintenaisiensis/mediterraneus, gigas* and then the modern *C. lupus*.

However, the ancestor of this lineage remains unknown and Brugal and Boudadi-Maligne (2011) considered that it may have originated from the local evolution of *C. mosbachensis*, or more likely from a distinct dispersal event.

The prospect of a true wolf lineage, separate from *C. etruscus-C. mosbachensis,* is interesting, and would offer a mechanism for explaining the large size of *C. lupus* as being a gradual development by way of the subspecies of *C. lupus*, and not an abrupt event. In contrast, in Pleistocene Britain, these subspecies have not been identified, and *C. lupus* is considered to be the only wolf present, albeit one with high intraspecific variation.

6.4.9. The position of this research

Based on the material analysed here and the evidence discussed, *C. etruscus, C. mosbachensis* and *C. lupus* are considered to be very likely related. In particular, *C. etruscus*

and *C. mosbachensis* were found to be similar in both size and ecology, and it therefore seems likely they formed a lineage of chronospecies in the Early to Middle Pleistocene.

The increase in the frequency and magnitude of climate shifts during the Middle Pleistocene, which provided a backdrop for the appearance of *C. lupus* in Europe, would have had a profound influence on the species. This contrasts with the relatively stable conditions that influenced both *C. etruscus* and *C. mosbachensis*.

It is therefore quite possible that the lineage was disrupted and that there is no simple procession of chronospecies. It seems that either locally-evolved *C. lupus* (most likely stemming from *C. mosbachensis*) was able to adapt quickly and flexibly to changing conditions (hence explaining its abrupt size increase), or that with changes in the carnivore community, *C. lupus* dispersed into Europe from an as-yet unknown locus, and is only distantly related to the *C. etruscus-C. mosbachensis* lineage.

The much larger size and apparent flexibility of *C. lupus* clearly sets it apart from these earlier canids and a branched wolf lineage may be the most parsimonious explanation.

C. mosbachensis is considered here to be a separate species to *C. lupus* on account of the statistically different craniodental variables analysed.

Although *C. etruscus* and *C. mosbachensis* seemed to be more similar ecologically, the cranio-dental measurements imply commonalities between *C. etruscus, C. arnensis* and *C. mosbachensis*, suggesting perhaps a more complicated relationship exists between these canids.

Although the existence of *C*. aff. *arnensis* is disputed by Garcia and Arsuaga (1999), as well as by the present study, based on the evidence from Boxgrove, the lack of *C. mosbachensis* specimens from southern European localities is notable. In order to make more informed inferences regarding the differences and similarities between these canids, a larger group of Early Pleistocene *C. mosbachensis* from southern Europe would need to be compared, supplemented by advances in ancient DNA extraction, should this prove possible, in order to clarify the ancestry of *C. mosbachensis* as well as its relationship to *C. lupus*.

7. Conclusions

The wolf, *C. lupus*, is an integral component of modern ecosystems, acting as an important regulator of large ungulates in the Palaearctic. This ultimately has indirect benefits for the ecosystem at large, preventing over-use of resources by herbivores and promoting greater biodiversity. Modern wolves are highly adaptable generalists and this great flexibility in diet is responsible for their persistence in the face of profound climatic, environmental and biotic change during the Pleistocene.

By using modern *C. lupus* as an analogue for Pleistocene *C. lupus* and the wolf-like canids, three research aims were devised in order to explore 1). how and why canid body mass has changed over the Pleistocene, 2). how and why canid ecology has changed over the Pleistocene, and finally 3). whether any further inferences on the evolutionary patterns within the wolf lineage could be made.

This research has created, for the first time, an extensive database of Pleistocene canid material over c. 1.8 Ma BP, particularly for Britain, and has applied multiple cranio-dental measurements to elucidate variation in body mass and palaeodiet both temporally, geographically and between the four key canid species of interest, *C. etruscus*, *C. arnensis*, *C. mosbachensis* and *C. lupus*.

Using a combination of body mass estimates and palaeodietary differences, the palaeoecology of the different canids was inferred, as well as their relationships to the contemporary larger carnivore community regarding potential prey selection and competitive interactions. *C. etruscus* and *C. mosbachensis* inhabited broadly equivalent, yet temporally disparate, ecological niches due to their similar body sizes and prey choices, and both were constrained by the presence of large and diverse felids as well as a larger canid; *C. falconeri* was coeval with *C. etruscus*, and *C.* (*X.*) *lycaonoides* was present with *C. mosbachensis*. By being smaller, *C. arnensis* was probably able to negate competitive interactions with both *C. etruscus* and *C. falconeri*. In contrast, on account of its much larger size, *C. lupus* was able to occupy a much higher position within the carnivore community of the later Pleistocene, which was also much reduced in diversity in comparison to the Early and early Middle Pleistocene.

The effects of palaeoclimatic shifts and associated palaeoenvironmental change on the different canid species was also examined, in order to evaluate whether any changes found at the species level were ultimately driven by climate change. The relative stability in the

body mass and diet of *C. etruscus* was related to the stable climatic conditions characterising the Early Pleistocene prior to the Mid Pleistocene Revolution (c. 1.2Ma). Although *C. mosbachensis* appeared similarly stable in its body size and diet between the late Early and early Middle Pleistocene, the more intense climatic fluctuations after 1.2Ma seemed to have had only a modest impact, and the constraining effect of large carnivores (especially the larger *C.* (*X.*) *lycaonoides*) may have been more important in keeping it morphologically and ecologically constant. However, the increasing intensity of climatic oscillations into the Late Pleistocene forced *C. lupus* to adapt, highlighted particularly by its increase in size and hypercarnivorous adaptations during MIS 5a.

Finally, by combining inferences on body mass change with in-depth morphological and morphometrical analysis, the validity of the proposed wolf lineage of *C. etruscus*, *C. mosbachensis*, and *C. lupus* was explored, in terms of whether *C. mosbachensis* was more related to *C. etruscus* (and hence the wolf-like lineage), or whether it was closer to *C. arnensis* (the coyote lineage). The relationship between *C. mosbachensis* and *C. lupus* was also investigated, particularly whether the controversial designation of *C. l. mosbachensis* as a subspecies can be justified. An alternative to the proposed wolf lineage was also considered, whereby *C. lupus* was more distantly related to the *etruscus-mosbachensis* line, and represented its own rapid dispersal from Eurasia rather than gradual evolution from *C. mosbachensis*.

7.1. How and why canid body mass changed over the Pleistocene

Based on m1 length, the estimated mean body masses of *C. etruscus* (24.34 ±1.65Kg), *C. arnensis* (17.94 ±1.73Kg) and *C. mosbachensis* (22.50 ±1.62Kg) were all smaller than those estimated for the Pleistocene *C. lupus* (35.81 ±1.59Kg). Because of the limited material available (Upper Valdarno only), it was not possible to establish body mass variation in *C. arnensis*.

Early Pleistocene *C. etruscus* was found to be slightly lighter at the younger site of Upper Valdarno (23.91 ± 1.69Kg) than at Olivola (25.55 ±2.70Kg), a slight decrease in size that may be related to the arrival of the canid competitors *C. arnensis* and *C. falconeri*. In particular, the arrival of a larger canid (*C. falconeri*) very likely affected *C. etruscus* by competing for similar prey. Thus by reducing in size slightly, *C. etruscus* was able to tolerate the presence of a larger canid and partition resources more effectively between them.

The mean estimated body masses of *C. etruscus* and *C. mosbachensis*, which first appeared during the late Early Pleistocene, were relatively similar, overlapping in their confidence intervals. Both were over the 21.5Kg dietary threshold, meaning that they could bring down prey larger than themselves, especially facilitated by assumed co-operative hunting behaviour. *C. mosbachensis* may therefore have occupied a similar position in the carnivore community as the older *C. etruscus*, with both species constrained in size and predatory choice by the presence of larger felids, as well as by the presence of larger hypercarnivorous canids; *C. falconeri* (for *C. etruscus*), and *C.* (*X.*) *lycaonoides* (for *C. mosbachensis*).

Although the sampling points are separated by around half a million years, *C. mosbachensis* from the British early Middle Pleistocene site of Westbury-sub-Mendip was similar to that from the German late Early Pleistocene site of Untermassfeld, at 22.35 ±1.90Kg and 23.14 ±1.71Kg respectively. This suggests relative stability in body mass, both temporally and geographically, reflecting not only apparent constancy in the contemporary carnivore community but also the presence of the land bridge connecting Britain to northern Europe.

However, it was interesting that *C. mosbachensis* at Boxgrove (20.34 ±18.50Kg) was found to be smaller in comparison to Westbury, although the precision of the estimate was low. Nonetheless the size difference perhaps represents localised variation at Boxgrove, with relatively smaller individuals dominating the site.

As a rule, body mass in *C. etruscus* and *C. mosbachensis* appears to have varied only minimally (within confidence interval ranges) during the Early and early Middle Pleistocene, with any minor oscillations potentially relatable to changes in the wider carnivore guild. For *C. etruscus*, relatively stable body mass may have also reflected stable palaeoclimatic conditions prior to the Mid Pleistocene revolution (c. 1.2 Ma). This stability engendered highly productive environments, which were able to support a large and diverse range of herbivore species, in turn sustaining a large and diverse carnivore community.

For *C. mosbachensis*, even though the onset of relatively more intense climatic change affected the chronological range of this species, the relative stability found in body mass between these episodes (material from temperate periods only was available) suggests that palaeoclimatic change may have had a lower impact. *C. mosbachensis* was able to migrate to more favourable conditions due to the terrestrial land bridge between Britain and northern Europe.

Further climatic deterioration characterised by more intense climatic episodes characterised the chronological range of *C. lupus,* which appeared during the late Middle Pleistocene (MIS 9 in Europe, MIS 7 in Britain). In contrast to the earlier Pleistocene canids, *C. lupus* in Britain was part of a greatly reduced carnivore guild, with *C. crocuta*, *P. leo*, *U. arctos* and very rare *P. pardus* the only other large carnivores present (notwithstanding the current controversy over the extension of *Homotherium* into the last cold stage). Thus, *C. lupus* was less constrained by multiple larger carnivores than at any previous time, and most notably, did not experience competition from another (larger) canid. Britain differed from the continent at this time, where the carnivore guild remained richer through the continued presence of *U. spelaeus* in the Late Pleistocene and also *C. alpinus* in some areas.

The body size of British *C. lupus* was also the most variable in comparison to earlier canids, both through time and within each individual age group. Generally, the late Middle Pleistocene and Late Interglacial wolves were slightly smaller than those of the Devensian, with reconstructed body masses of 34.03 ±1.73Kg for MIS 7, 32.18 ±2.70Kg for MIS 6 and 33.54 ±2.70Kg for MIS 5e, contrasting with 35.20kg for MIS 5c in the very early Devensian, 39.85 ±1.64Kg for MIS 5a, 35.40 ±1.63Kg for MIS 3 and 38.57kg for MIS 2. Although fluctuations were present, especially during MIS 5a, a slight trend towards increasing size may therefore be noted through the Devensian.

The body mass estimates of Pleistocene *C. lupus* were smaller than for its modern counterpart (mean body mass of species 41.33Kg), although all lay within its large modern size range (18-80Kg [Mech, 1974]). The increasing size trend noted here through the Devensian is thus consistent with the eventual large size reached by modern northern European wolves, suggesting continued increase in size into the Holocene.

The continual fluctuation in *C. lupus* body size through the Pleistocene foreshadowed the flexibility in body size apparent today. Body size variation was also present within individual age groups in Britain, indicating strong intra-species variability, perhaps related to regional differences creating locally distinct populations or to the effects of rapid palaeoclimatic oscillations. Ultimately, flexibility in body size represented a successful adaptive response to coping with both local and broader palaeoecological change.

Due to the higher numbers of individuals available, as well as the corresponding detailed evidence of prevailing palaeoclimatic and palaeoenvironmental conditions, particular attention was paid to MIS 7, 5a and 3 throughout this research. Interestingly, wolves from MIS 7 (the penultimate interglacial) and 3 (the Middle Devensian) were found to be more

similar in size when compared to the much larger animals from MIS 5a, especially considering the general trend towards increasing body mass through the last cold stage. The resemblance in body size between MIS 7 and 3 is thought to reflect relative palaeoenvironmental similarity between these two climatic stages, in particular the presence of open grassland environments, as well as a comparable carnivore community structure and prey spectrum.

The much larger wolves found during MIS 5a were apparently related to a unique combination of variables. Notably, the severely cold climatic conditions may have caused a Bergmannian response leading to increase in size, with wolves further 'liberated' by an absence of lion and spotted hyaena in Britain at this time. The combination of low prey species diversity and harsh conditions meant that competition was doubtless extremely high, both from the very large brown bear present, as well as from other wolves and from smaller predators such as wolverine and perhaps arctic fox. The larger body size may therefore also have conferred a competitive advantage on wolves.

In light of this, it would be interesting to examine wolves from pre-Devensian cold climatic episodes to see whether a Bergmannian response was equally present. Although wolves from MIS 6 were analysed in the present research, material was very sparse and only representative of one site (Clevedon Cave) for the extended duration of the cold stage

The body mass reduction seen in *C. lupus* by MIS 3, although remaining within the general Devensian trend of size increase, may have been an adaptive response to more environmentally favourable conditions, as well as the return of larger competing carnivores. With the return to Britain of spotted hyaena and lion, *C. lupus* may have been unable to maintain its dominance in their presence.

The interplay between climate, ecology and competition were therefore important factors in controlling body size in all the analysed canids. When carnivore diversity was high, wolves remain relatively modest in body mass. However, as soon as the constraining effect of large felids, hyaenids and other canids is removed, wolves experience an increase in body mass, augmented by a Bergmannian response to palaeoclimatic deterioration in the Late Pleistocene. Nevertheless, these changes in body size were often also reflected by variation in diet, especially in *C. lupus*.

In terms of gauging the level of sexual dimorphism in the Pleistocene canids, due to the difficulties in separating fragmentary fossil material by sex, sexual dimorphism in *C.*

mosbachensis, C. etruscus and *C. arnensis* could not be examined. The presence of sexual dimorphism in the sexed modern wolf dataset was therefore explored, with sexual dimorphism in cranio-dental characters found to be low, varying from 2.27% – 8.02% in a sample of measurements including p4l, m1L, m1W, m2L, p1m3L, m1m2D, P4L, P4W, M1L, M1W, M1M2L and SKL.

However, when compared to a study of sexual dimorphism in wolves from Israel based on the lower carnassial and condylobasal skull length by Dayan et al. (1992), the European wolves were found to be slightly more sexually dimorphic in these measurements (lower carnassial: 3% [Dayan *et al*., 1992], 6.94% this present study; skull length: 3% [Dayan *et al*., 1992], 4.81% this study). The interplay of Bergmann's rule and sexual dimorphism may be behind the differences found between Europe and Israel, however as the driving forces behind both mechanisms are complex, further investigation is needed to understand this relationship.

Nonetheless, based on the relatively low level of sexual dimorphism found in modern *C. lupus*, Pleistocene *C. lupus* is unlikely to have been more sexually dimorphic. It is therefore likely that the Pleistocene canids analysed here may have followed the canid trend of having generally low-level but nevertheless present sexual dimorphism.

7.2. How and why changes in diet occurred over the Pleistocene

Based on a suite of dietary-diagnostic cranio-dental measurements, the palaeodiet of the Pleistocene canids was inferred, based on their different abilities to slice flesh, crush non-flesh foods, crack bone and withstand the stress of hunting large prey.

The cranio-dental measurements indicated that the medium-sized *C. etruscus* had the most omnivorous diet, based on its enhanced ability to crush non-flesh foods, combined with some ability to slice flesh as also evidenced by its comparatively weak jaws. Nevertheless, since it was above the dietary threshold weight, *C. etruscus* likely hunted prey larger than itself, aided by cooperative hunting.

However, in contrast to body size, where slight difference was noted between the Early Pleistocene sites of Olivola and the Upper Valdarno, no difference in diet was found between these two sites, nor were there significant differences in the frequency of tooth wear and breakage. The lack of difference is interpreted here as evidence for dietary

stability, which was apparently not impacted by the arrival of *C. falconeri* and *C. arnensis* by the Upper Valdarno, both of which were relatively more carnivorous than *C. etruscus*.

Although no temporal comparison of diet was possible for *C. arnensis*, it was interpreted as having a more omnivorous diet than *C. mosbachensis*, but perhaps less than *C. etruscus*. Unlike the hypercarnivorous canids, it was less able to slice flesh quickly and possessed only weak jaws, which when combined with its smaller body size (below the dietary threshold weight), indicated that *C. arnensis* likely hunted small prey.

In terms of the Van Valkenburgh (1988a) dietary categories, the diets of both *C. etruscus* and *C. arnensis* can be differentiated further than simply '>70% meat', as considered by Cherin et al. (2013b). Although these dietary categories were intended to be broad in order to encompass a wide range of carnivorous diets, for *C. etruscus* and *C. arnensis* this category is misleading, as both were found to be more omnivorous, incorporating a larger range of non-flesh foods into their diets, such as fruit and vegetable matter. The smaller size of *C. arnensis* below the 21.5Kg dietary threshold also suggests a diet of smaller mammals and invertebrate prey may have been more significant.

Again, relatively stable climatic conditions through the Early Pleistocene fostered the development of highly productive environments, which were able to support both a diverse range of prey and carnivores, including the coexistence of several canids, to which *C. mosbachensis* was added during the late Early Pleistocene.

The diet of *C. mosbachensis* was found to be more carnivorous than that of *C. etruscus*, based on this canid having lower crushing ability for non-flesh foods. It possessed relatively weak jaws, corresponding with its medium size, and its ability to slice flesh rapidly was perhaps slightly less than *C. etruscus*. Although slightly smaller than *C. etruscus*, *C. mosbachensis* was also just above the dietary threshold and was therefore able to take prey larger than itself.

Based on their broadly similar size and morphology, *C. mosbachensis* likely filled a similar role in the carnivore community to *C. etruscus*. However, the increased carnivory apparent in *C. mosbachensis* may have been in response to the presence of the larger and more hypercarnivorous *C.* (*X.*) *lycaonoides*, thus enabling *C. mosbachensis* to increase its flesh consumption following the dietary shift in the canid above it in the carnivore community.

Although no temporal differences in the diet of *C. mosbachensis* were found, differences in the frequency of tooth wear were present between Untermassfeld and British MIS 13 sites.

The reasons behind this, however, are not apparent. As no variation in diet was found between these sites, and all sites represent temperate conditions, climatic conditions are not thought to influence tooth wear differences. All sites are characterised by high species diversity, as well as similar levels of carnivore competition from larger felids as well as a larger canid, *C.* (*X.*) *lycaonoides*. Thus perhaps the higher incidences of heavily worn teeth found at Untermassfeld relate to a tendency for wolves to engage in leisurely bone chewing in contrast to active bone cracking or crunching.

The overall constancy in diet for *C. mosbachensis* (similar to *C. etruscus*), may be the result of relatively stable palaeoclimatic conditions through most of its temporal range. However, the slight differences in tooth wear and fluctuations in body mass through time may reflect the climatic deteriorations experienced since the Mid Pleistocene Revolution, together with increasing potential for the development of local populations, especially after the breaching of the Strait of Dover during MIS 12.

From the cranio-dental measurements, the diet of Pleistocene *C. lupus* was typically generalist, with an increased ability to slice flesh, crack bone, crush non-flesh foods, and capture large prey with its strong jaws, in comparison to the other Pleistocene canids. Like its modern counterpart, *C. lupus* was consistently larger than the dietary threshold weight, and aided by cooperative hunting, was able to capture prey much larger than itself.

However, as with the variation in body mass observed in British *C. lupus*, temporal differences in diet were also present between MIS 7, 5a, 3 and in comparison to a dataset of modern Swedish wolves. The similarity in estimated body masses between MIS 7 and 3 was echoed by dietary similarity during these two episodes, highlighted by the presence of weaker jaws than seen in both MIS 5a and modern wolves, a reduced capacity to slice flesh quickly and more adaptation for crushing of non-flesh foods.

The similar palaeoecological conditions and range of carnivore competitors between MIS 7 and 3 engendered similar adaptive responses in diet from *C. lupus*, in particular the relatively temperate conditions (even for Middle Devensian summers) would have provided a more diverse range of plant and invertebrate foods. However, the unusual palaeogeographic and restricted biotic conditions of MIS 5a in Britain required a heightened adaptive response, with MIS 5a *C. lupus* becoming better adapted for fast flesh slicing than non-flesh food crushing, combined with higher bone cracking ability and broader jaws for manipulating large prey. High frequencies of tooth breakage and wear

were also common at this time, a function of the harsh environmental conditions and elevated levels of competition.

The absence of lion and spotted hyaena during MIS 5a were also important in terms of wolf diet, by apparently allowing *C. lupus* behavioural flexibility through broadening its niche to include increased meat slicing, scavenging and bone consumption.

The dietary flexibility and adaptability are highlighted by the dietary differences observed between Pleistocene *C. lupus* and modern Swedish wolves. Perhaps a function of the more boreal environment, together with a very different and impoverished large carnivore community, modern Swedish *C. lupus* were found to have an increased ability to slice flesh (likely quicker than in both MIS 7 and 3), as well as an increased ability to crush non-flesh foods. Some ability to crack bone was also present, although not to the same extent as seen in MIS 5a. Finally, the Swedish wolves also had strong deep jaws enabling the capture of large sized prey.

Although climates in both MIS 7 and the present day are interglacial, vegetational differences are apparent. Late MIS 7 was characterised by largely open grassland environments supporting large herds of herbivores, whereas modern Sweden is characterised by boreal forest, with large herbivore prey present but in much more dispersed herds. Modern wolves therefore need a combination of adaptation, in order to take advantage of non-flesh resources but also to be able to bring down large prey if and when the chance arises.

Although both lion and spotted hyaena are now absent in Europe, other large carnivores such as *U. arctos* and *L. lynx* are both present in Sweden, as well as the smaller *G. gulo*, which all target the ungulate prey present such as Eurasian elk and reindeer (albeit this habit is more seasonal for brown bear, and wolverines tend to scavenge more from wolf kills). Thus, although competition was likely more intense from other social carnivores of the Pleistocene, competition from the modern members of the carnivore guild in Europe nonetheless still affects modern *C. lupus* to some extent, in terms of selecting similar resources.

For the Pleistocene, underpinning the temporal variation in both body mass and ecology were the dramatic and intense shifts in climatic conditions characterising the later Pleistocene, and the resultant effect this had on environment type and species diversity. Thus the ability of *C. lupus* to adapt flexibly to these changes is testament to their success

as a carnivore and indeed, a key reason why they have persisted where others have become extinct.

7.3. The wolf lineage

The validity of a postulated wolf lineage consisting of the chronospecies *C. etruscus, C. mosbachensis*, and *C. lupus* was discussed with reference to the morphological findings and body mass reconstructions in this research.

Both *C. etruscus* and *C. mosbachensis* are here considered as wolf-like, sharing key morphological characters such a lower positioned p3 in the mandible in comparison to the adjacent p2 and p4, accessory cusps present posteriorly on the p4, similarly developed crests present on the m1 talonid, as well as a pronounced anterior buccal cingulum below the paraconid on the m2. The two species displayed statistical similarity in many of the cranio-dental measurements and were thus assumed to occupy broadly similar niches.

Although *C. lupus* shares the more complex talonid morphology, this feature was much more variable within the species, both Pleistocene and modern. In general, *C. lupus* also had much larger and broader cranio-dental morphology compared to the other Pleistocene canids, and was notably statistically different in all cranio-dental measurements. It is therefore perhaps too simplistic to include all three canids into one lineage since *C. lupus* is consistently different from the earlier Pleistocene canids.

No evidence was found of *C. mosbachensis* gradually increasing in size and becoming *C. lupus*, as originally proposed by the wolf lineage, with late Middle Pleistocene *C. mosbachensis* from mainland European sites of similar size to its early Middle Pleistocene counterparts. Perhaps related to this is the idea that *C. lupus* had an apparently abrupt arrival in Europe according to Rook and Torre (1996a), from an as-yet unknown Eurasian origin.

It is therefore possible that *C. lupus* may not have directly evolved from the *etruscus-mosbachensis* lineage, as also proposed by Brugal and Boudadi-Maligne (2011) who considered that the presence of the 'true' wolf lineage in western Europe started with *C. l. lunellensis* in the late Middle Pleistocene. Although *C. lupus* is considered as the only wolf present in Pleistocene Britain here, albeit one with high intraspecific variability, it is nonetheless possible that *C. lupus* originated from its own distinct dispersal event.

C. mosbachensis was also considered here to be a separate species to *C. lupus* rather than a subspecies, since although some morphological affinity was present as outlined above, the two taxa were statistically different in all analysed cranio-dental measurements, with a much closer affinity with *C. etruscus*.

7.4. Limitations of this research

The limitations of this research relate to problems with incomplete material and sample size, the dating of sites for the European mainland and the regional spread of data.

A common problem in palaeontological research is incomplete material and this study was no different in that much of the material analysed was inevitably fragmentary. This impacted directly on body mass estimation, since carnassial length was chosen above other (possibly better) predictive characters, on account of the relative abundance of m1s in all four canid species. The limitations of using m1 length in body mass estimation are well known but the benefits of its use here, and the resultant ecological inferences, were considered to outweigh its potential problems.

With respect to sample sizes, although all available cranial and postcranial material was recorded and measured during this research, further statistical analysis was frequently not possible because of limited availability of comparable specimens. Again, small sample sizes in palaeontological research are frequently unavoidable. Here, the main problems occurred when material from an individual age group was under-represented, rendering temporal comparisons sometimes difficult. For this reason, it was necessary to focus analysis of palaeodiet in *C. mosbachensis* in Britain on MIS 13 alone, and in *C. lupus* on MIS 7, 5a and 3, where the most abundant datasets were present.

The vagaries of the fossil record also affect the assessment of change through time, since sampling points for *C. mosbachensis* were separated by around half a million years between Untermassfeld and the Cromerian Complex sites in Britain. The geographical bias also proved an issue for interpreting the place of *C. mosbachensis* within the wolf lineage, since the predominance of northern European material limited assessment of its possible relationship with the putative *C.* aff. *arnensis* from southern Europe. Similarly, although Early Pleistocene material from Germany and Italy was analysed, there was a lack of comparable data from the rest of Europe, in particular from northwest and southern regions. For *C. lupus*, comparisons of British material with that from mainland Europe were

also limited mainly to Germany on account of sample access and availability. Comparisons with wolves from more geographically-proximal countries in particular might have been potentially illuminating.

On the other hand, sites may often be too closely clustered to see differences through time, for example Westbury sub Mendip and Boxgrove *C. mosbachensis*, and *C. etruscus* from the Olivola and Tasso F.U.s.

Even when sites are present, the lack of dating was also problematic, chiefly for Late Pleistocene *C. lupus* in mainland Europe. The necessary use of broad age groups to enable analysis here was the only way to create large enough datasets for comparative analysis with Britain. A lack of dated material was also problematic in some circumstances for Britain, since some specimens had to be excluded from analysis because of an absence of geochronological or other dating support. These sites therefore potentially represent information figuratively 'lost' to the analysis.

In the analysis of modern *C. lupus*, the assessment of latitudinal size clines in modern European wolves was limited by the lack of southern European members within the dataset. To fully compare the differences between high-latitude Swedish wolves and their southern counterparts, a more comprehensive southern European wolf dataset was needed but was impossible to obtain because of time and other constraints.

The influence of body size on the diet-related cranio-dental measurements was a key issue in this research. Although attempts were made to counteract their influence (e.g. by employing Mosimann shape variables), there are inherent problems with the use of ratios to negate its effects. Thus body size is likely to be exerting at least some influence on the dietary differences between the four canids but it is difficult to quantify how important this effect is. That said, body size and diet are intimately related and ultimately for carnivores, body size has a strong influence over prey choice, as well as dictating dietary morphology and adaptations. Hence, an attempt to disassociate size and diet may result in a less accurate representation of a species.

7.5. Future work

There is much scope for further research into the Pleistocene canids of Europe. The chronology of their first and last appearances, their phylogenetic relationships, questions relating to sympatry and competition, and adaptations to abrupt climatic and

environmental change are of great significance not only for interpreting the changing role of a key Pleistocene predator but also for conservation of modern wolves. The present research has provided a testable model that can be constantly assessed and updated with the discovery of new sites and material.

Britain in particular has an extremely rich record of both *C. mosbachensis* and *C. lupus* and a well-constrained chronology within which to examine temporal and interspecific change. For *C. mosbachensis*, further comparison with coeval southern European localities would be interesting. It would also be useful, if new material became available from sites of MIS 11 and 9 age, to compare differences within this species between pre-Anglian (MIS 12) populations and those of the later Middle Pleistocene.

For *C. lupus*, a future line of investigation would be to examine other neighbouring European sites correlated with MIS 5a, in order to establish what effect island isolation in Britain had on these highly adapted wolves. Currently, no wolf material is known in Britain from MIS 4 but if discovered, it would be interesting to examine these populations to see whether the features seen in MIS 5a persisted and how quickly the 'return' to the form present during MIS 3 was. It would also be illuminating to analyse Holocene wolf material, in order to explore the impacts of post LGM climatic warming, subsequent reforestation in Europe and resultant changes to the mammalian community.

From the first appearance of *C. lupus* during the late Middle Pleistocene, wolves have been immensely successful due to their high level of cranio-dental plasticity and incredibly flexible ecology, enabling their continued survival throughout the dramatic oscillations in Pleistocene climate. Wolves are keystone predators, having an extremely important ecological role in top-down regulation of ungulate prey, something that needs increased recognition in the light of ongoing large carnivore persecution. Nonetheless, as attitudes to the importance of large predators slowly improve and legislative protection from undue human interference increases, the exceptional ability of wolves to adapt to changing ecological, environmental and climatic conditions bodes well for their future.

Bibliography

Abouheif, E. and Fairbairn, D.J. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *The American Naturalist*. **149(3)**, 540-562

Adam, K. D. (1975). Die mittelpleistozäne Säugetier-Fauna aus dem Heppenloch bei Gutenberg (Württemberg). *Stuttgarter Beitrage zur Naturkunde Serie B (Geologie und Paläontologie)*. **3**, 1-141.

Albrecht, G.H. 1978. Some comments on the use of ratios. *Systematic Zoology.* **27(1)**, 67-71.

Alroy, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. *Science.* **280**, 731-734.

Andersson, K. and Werdelin, L. 2003. The evolution of cursorial carnivores in the Tertiary: implications of elbow joint morphology. *Proceedings of the Royal Society, London. B*. **270**, S163-S165.

Andersson, K. 2004a Predicting carnivoran body mass from a weight-bearing joint. *Journal of Zoology, London.* **262**, 161-172.

Andersson, K. 2004b. Elbow-joint morphology as a guide to forearm function and foraging behaviour in mammalian carnivores. *Zoological Journal of the Linnean Society*. **142**, 91-104.

Andersson, K. 2005. Were there pack-hunting canids in the Tertiary, and how can we know? *Paleobiology*. **31(1)**, 56-72.

Andrews, P. and Cook, J. 1999. Description of the sedimentary sequence at Westbury Cave. In: Andrews, P., Cook, J., Currant, A. P. & Stringer, C. (eds.). *Westbury Cave. The Natural History Museum excavations 1976-1984*. CHERUB. Western Academic & Specialist Press Ltd. 19-59.

Ansorge, H., Kluth, G. and Hahne, S. 2006. Feeding ecology of wolves *Canis lupus* returning to Germany. *Acta Theriologica*. **51(1)**, 99-106.

Anton, M., Galobart, A. and Turner, A. 2005. Co-existence of scimitar-toothed cats, lions and hominins in the European Pleistocene. Implications of the post-cranial anatomy of *Homotherium latidens* (Owen) for comparative palaeoecology. *Quaternary Science Reviews.* **34**. 1287-1301.

Anyonge, W. 1993. Body mass in large and extant carnivores. Journal *Journal of Zoology, London*. **231(2)**, 339-350.

Anyonge, W. 1996. Locomotor behaviour in Plio-Pleistocene sabre-tooth cats: a biomechanical analysis. *Journal of Zoology*. **238(3)**, 395-413.

Anzidei, A.P., Bulgarelli, G.M., Catalano, P., Cerilli, E., Gallotti, R., Lemorini, C., Milli, S., Palombo, M.R., Pantano, W. and Santucci, E. 2011. Ongoing research at the late Middle Pleistocene site of La Polledrara di Cecanibbio (central Italy), with emphasis on human-elephant relationships. *Quaternary International*. **255**, 171-187.

Argant, A. 2009. Biochronologie et grands mammifères au Pléistocène moyen et supérieur en Europe occidentale: l'apport des Canidés, des Ursidés et des Carnivores en général. *Quaternaire*. **20(4)**, 467-480.

Arribas, A. and Palmqvist, P. 1998. Taphonomy and palaeoecology of an assemblage of large mammals: hyaenid activity in the lower Pleistocene site at Venta Micena (Orce, Guadix-Baza Basin, Granada, Spain). *Geobios*. **31**, 3-47.

Arnborg, T. 1990. Forest types of northern Sweden, introduction to and translation of 'Det nordsvenska skogstypsschemat'. Vegatatio. **90**, 1-13.

Arzarello, M., Marcolini, F., Pavia, G., Pavia, M., Petronio, C., Petrucci, M., Rook, L. and Sardella, R. 2009. The lithic industry of the Early Pleistocene site of Pirro Nord (Aprecena, south Italy): the evidence of a human occupation between 1.3 and 1.7 Ma. *L'anthropologie*. 113, 47-58.

Asa, C. and Cossios, E.D. 2004. Sechuran fox *Pseudalopex sechurae.* In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 69-72.

Asa, C.S., Valdespino, C. and Cuzin, F. 2004. Fennex fox *Vulpes zerda*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 205-209.

Ashton, K. G., Tracy, M. C. and de Queiroz, A. 2000. Is Bergmann's rule valid for mammals? *The American Naturalist*. **156(4)**, 390-415.

Atchley, W.R., Gaskins, C.T. and Anderson, D. 1976. Statistical properties of ratios. I. Empirical results. *Systematic Zoology.* **25**, 137-148.

Atchley, W.R. 1978. Ratios, regression intercepts and the scaling of data. *Systematic Zoology.* **27(1)**, 78-83.

Atkinson, R.P.D. and Loveridge, A.J. 2004. Side-striped jackal *Canis adustus*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 152-156.

Atkinson, T.C., Briffa, K.R. and Coope, G.R. 1987. Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature*. **325**, 587-592.

Azzaroli, A. 1983. Quaternary Mammals and the 'End Villafranchian' dispersal event – a turning point in the history of Eurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **44**, 117-138.

Azzaroli, A., De Giuli, C., Ficcarelli, G. and Torre, D. 1988. Late Pliocene to Early Mid-Pleistocene mammals in Eurasia: Faunal succession and dispelrsal events. *Palaeogeography, Palaeoclimatology, Palaeoecology.* **66**, 77-100.

Ballard, W. B., Cronin, M. A., Robards M. D. and Follmann, E. H. 2000. Body sizes, ages, reproductive status, and sex ratios of arctic foxes, *Alopex lagopus*, in the Prudhoe Bay oil field, Alaska. *Canadian Field-Naturalist*. **114**, 493–494.

Ballard, W.B., Carbyn, L.N. and Smith, D.W. 2003. Wolf interactions with non-prey. In: Mech, L.D. and Boitani, L. (eds.). Wolves: behaviour, ecology and conservation. The University of Chicago Press, USA. 259.

Barnett, R., Shapiro, B., Barnes, I. Ho, S.Y.W., Burger, J., Yamaguchi, N., Higham, T.F.G., Wheeler, H.T., Rosendahl, W., Sher, A.V., Sotnikova, M., Kuznetsova, T., Baryshnikov, G.F., Martin, L.D., Harrington, C.R., Burns, J.A. and Cooper, A. 2009. Phylogeography of lions (*Panthera leo* ssp.) reveals three distinct taxa and a late Pleistocene reduction in genetic diversity. *Molecular Ecology*. **18**, 1668-1677.

Baryshnikov, G.F. and Boeskorov, G.G. 2004. Skull of the Pleistocene brown bear (*Ursus arctos*) from Yakutia, Russia. *Russian Journal of Theriology*. **3(2)**, 71-75.

Baryshnikov, G. F. and Tsoukala, E. 2010. New analysis of the Pleistocene carnivores from Petralona Cave (Macedonia, Greece) based on the Collection of the Thessaloniki Aristotle University. *Geobios*. **43(4)**, 389-402.

Bauer, H., Nowell, K. and Packer, C. 2012. *Panthera leo*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Downloaded on **26 August 2013**.

Bateman, J.A. Faunal remains from Ogof yr Ychen, Caldey Island. *Nature*. **(245)**, 454-455.

Begon, M., Towsend, C.R. and Harper, J.L. 2006. Ecology: from individuals to ecosystems. Blackwell Publishing, Oxford, U.K.

Bekoff, M. 1977. *Canis latrans. Mammalian Species*. **79**, 1-9.

Benton, M.J. 2002. Cope's Rule. In: Pagel, M. (ed.) *Encyclopedia of Evolution*. Oxford University Press, Oxford, U.K. pp 185-186.

Bergmann, C. 1847. Ueber die verhältnisse der wärmeökonomie der thiere zu ihrer grösse. *Gottinger studien*. **3**, 595-708

Berta, A. 1987. Origin, diversification zoogeography of South American Canidae. *Fieldiana Zoology.* **39**, 455-471.

Bertini, A. 2003. Early to Middle Pleistocene changes of the Italian flora and vegetation in the light of a chronostratigraphic framework. *Il Quaternario*, **16(1)**, 19-36.

Bertini, A., Ciaranfi, N., Marino, M. and Palombo, M.R. 2010. Proposal for Pliocene and Pleistocene land-sea correlation in the Italian area. *Quaternary International*. **219**. 95-108.

Bertini, A. 2013. Climate and vegetation in the Upper Valdarno Basin (central Italy) as a response to Northern Hemisphere insolation forcing and regional tectonics in the late Pliocene-early Pleistocene. *Bollettino della Società Paleontologica Italiana*. **132(1)**, 137-148.

Binder, W. J., Thompson, E. N., Van Valkenburgh, B. 2002. Temporal variation in tooth fracture among Rancho La Brea dire wolves. *Journal of Vertebrate Paleontology*. **22(2)**, 423-428.

Bishop, M.J. 1974. A preliminary report on the Middle Pleistocene mammal bearing deposits of Westbury-sub-Mendip, Somerset. *Proceedings of the University of Bristol Spelaeological Society*. **13**, 301-318.

Bishop, M. J. 1982. The mammalian fauna of the early Middle Pleistocene cavern infill site of Westbury-sub-Mendip, Somerset. *Palaeontological Association.* Special Publication **28**. Pp 108.

Blanckenhorn, W.U., Stillwell, R.C., Young, K.A., Fox, C.W. and Ashton, K.G. 2006. When Rensch meets Bergmann: does sexual size dimorphism change systematically with latitude? *Evolution*. **60(10)**, 2004-2011.

Blackwell, B. and Schwartz, H. P. 1986. U-series analyses of the Lower Travertine at Ehringsdorf, DDR. *Quat. Research.* **25**. 215-222.

Bocherens, H., Drucker, D. G., Bonjean, D., Bridault, A., Conard, N. J., Cupillard, C., Germonpré, M., Höneisen, M., Münzel, S.C., Napierala, H., Patou-Mathis, M., Stephan, E., Uerpmann, H-P. and Ziegler, R. 2011. Isotopic evidence for dietary ecology of cave lion (*Panthera spelaea*) in North-Western Europe: Prey choice, competition and implications for extinction. *Quaternary International*. **245(2)**, 249-261.

Bocquet-Appel, J-P. and Demars, P.Y. 2000. Neanderthal contraction and modern human colonisation of Europe. *Antiquity*. **74(285)**, 544-552.

Bogaert, R. van, Haneca, K., Hoogesteger, J., Jonasson, C., De Dapper, M. and Callaghan, T.V. 2011. A century of tree line changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *Journal of Biogeography.* **38**, 907-921.

Boismier, W., Schreve, D. C., White, M. J., Robertson, D. A., Stuart, A. J., Etienne, S., Andrews, J., Coope, G.R., Field, M., Green, F.M.L., Keen, D.H., Lewis, S.G., French, C.A., Rhodes, E., Schwenninger, J.L., Tovey, K. and O'Connor, S. 2003. A Middle Palaeolithic site at Lynford Quarry, Mundford, Norfolk: interim statement. *Proceedings of the Prehistoric Society.* **69**, 314-324.

Bollen, K.A. and Jackman, R.W. 1990. Regression diagnostics: an expository treatment of outliers and influential cases. In: Fox, J. and Long, J.S. (eds.). *Modern methods of data analysis*. Sage Publications, U.S.A. Pp 257-291

Bon, M., Piccoli, G. and Sala, B. 1991. I Giacimenti Quaternari di vertebrati fossili nell'Italia norf-orientale. *Memorie di Scienze Geologiche, Padova*. **XL111.** 185-231.

Borgognini Tarli, S.M., Fornaciari, G. and Palma di Cesnola, A. 1980. Restes humains des niveaux gravettiens de la Grotte Paglicci (Rigano Garganico): context archéologique, etude anthropologique et notes de paléopathology. *Bulletins et Mémoires de la Société d'anthropologie de Paris.* **XIII (7)**, 125-152.

Boudadi-Maligne, M. 2012. A new subspecies of wolf (*Canis lupus maximus nov. subsp.*) from the upper Pleistocene of Western Europe. *Comptes Rendus Palevol*, **11**, 475-484.

Bowen, D.Q., Rose, J., McCabe, A.M. and Sutherland, D.G. 1986. Correlation of Quaternary glaciations in England, Ireland, Scotland and Wales. *Quaternary Science Reviews*. **5**, 299-340.

Bowen, D.Q., Lewis, S.G., Maddy, D., Gibbard, P.L., Preece, R.C., Campbell, S., Thomas, G.S.P., Sutherland, D.G., McCabe, A.M., Cameron, T.D.J. and Holmes, R.A. 1999. A revised correlation of Quaternary deposits in the British Isles. *Geological Society Special Report*. **23**.

Boyd, D. K., Ream, R. R., Pletscher, D. H., Fairchild, M. W. 1994. Prey taken by colonising wolves and hunters in the Glacier National Park Area. *The Journal of Wildlife Management*. **58(2)**, 289-295.

Boylan, P. J. 1981. A new revision of the Pleistocene mammalian fauna of Kirkdale Cave, Yorkshire. *Proc. Yorks. Geol. Soc*. **43(3)**. 253-280.

Bratlund, B. 1999. Taubach revisited. *Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz*. **46(2000)**, 61-174.

Breitnmoser, U. 1998. Large predators in the Alps: the fall and rise of Man's competitors. *Biological Conservation*. **83(3)**, 279-289.

Bridgland, D. R. 1998. The Pleistocene history and early human occupation of the river Thames valley. In Ashton, N., Healy, F. and Pettitt, P. (Eds.) *Stone Age Archaeology. Essays in honour of John Wymer*. Oxbow Books. Pp 29-37.

Brown, J.H. 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. *American Zoologist*. **21(4)**, 877-888.

Brown, W. L. and Wilson, E. O. 1956. Character displacement. *Systematic zoology*. **5(2)**, 49-64.

Brugal, J-P., Boudadi-Maligne, M. 2011. Quaternary small to large canids in Europe: Taxonomic status and biochronological contribution. *Quaternary International*. **243(1)**, 171-182.

Brunnacker. K., Jäger, K.D., Hennig, G.J., Preuss, J. and Grün, R. 1983. Radometrische Untersuchungen zur Datierung mitteleuropaischer Travertinvorkommen. *Ethnographisch-Archäologisch Zeitschrift*. **24**, 217-266.

Bueler, L. E. 1973. *Wild dogs of the world.* Stein and Day, New York. Pp 274.

Burger, J., Rosendahl, W., Loreille, O., Hemmer, H., Eriksson, T., Gotherstrom, A., Hiller, J., Collins, M.J., Wess, T. and Alt, K.W. 2004. Molecular phylogeny of the extinct cave lion *Panthera leo spelaea*. *Molecular Phylogenetics and Evolution*. **30**, 841-849.

Burleigh, R., Matthews, K. and Ambers, J. 1982. British Museum natural radiocarbon measurements XIV. *Radiocarbon*. **24(3)**. 229-261.

Busschers, F.S., Van Balen, R.T., Cohen, K.M., Kasse, C., Weerts, H.J.T., Wallinga, J. and Bunnik, F.P.M. 2008. Response of the Rhine-Meuse fluvial system to Saalian ice-sheet dynamics. *Boreas*. **37**, 377-398.

Callaghan, T.V., Björn,L.O., Chernov,Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R.A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G., Elster, J., Henttonen, H., Laine, K., Taulavuori, K., Taulavuori, E. and Zöckler, C. 2004. Biodiversity, distributions and adaptations of Arctic species in the context of environmental change. *AMBIO*. **33(7)**, 404-417.

Caloi, L. and Palombo, M.R. 1997. Biochronology of large mammals in the Early and Middle Pleistocene of the Italian peninsula. *Hystrix*. **9(1-2)**, 3-12.

Campbell, S. and Bowen, D. O. 1989. *Quaternary of Wales*. Geological Conservation Review. Pp 237.

Campbell, S. and Stuart, A. J. 1998. Joint Mitnor Cave. In: Campbell, S., Hunt, C. O., Scourse, J. D. and Keen, D. H. (eds.). *Quaternary of south-west England*. Geological Conservation Review Series. Chapman & Hall. 149-155.

Candy, I. and Schreve, D. 2007. Land–sea correlation of Middle Pleistocene temperate sub-stages using high-precision uranium-series dating of tufa deposits from southern England. *Quaternary Science Reviews*. **26(9)**, 1223-1235.

Candy, I., Coope, G.R., Lee, J.R., Parfitt, S.A., Preece, R.C., Rose, J. and Schreve, D.C. 2010. Pronounced warmth during early Middle Pleistocene interglacials: investigating the Mid-Brunhes Event in the British terrestrial sequence. *Earth-Science Reviews*. **103**, 183-196.

Capitani, C., Bertelli, I., Varuzza, P., Scandura, M. and Apollonio, M. 2003. A comparative analysis of wolf (Canis lupus) diet in three different Italian ecosystems. *Mammalian Biology*. **69(1)**, 1-10.

Carbone, C., Mace, G.M., Craig Roberts, S. and MacDonald, D.W. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature*. **402**, 286-288.

Caro, T.M. and Stoner, C.J. 2003. The potential for interspecific competition among African carnivores. *Biological Conservation.* **110**, 67-75.

Caro, T. 2005. The adaptive significance of colouration in mammals. *BioScience*. **55(2)**, 125-136.

Caso, A., Lopez-Gonzalez, C., Payan, E., Eizirik, E., de Oliveira, T., Leite-Pitman, R., Kelly, M., Valderrama, C. and Lucherini, M. 2008. *Puma concolor*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Downloaded on **27 August 2013**.

Cavallini, P. 1995. Variation in the body size of the red fox. *Annales Zoologici Fennici*. **32**, 421-427.

Chesemore, D. L. 1975. Ecology of the arctic fox (Alopex lagopus) in North America—a review. In: Fox, M.W. *The Wild Canids. Their systematics, behavioural ecology and evolution. Van Nostrand Rheinhold, New York.* Pp 143-163.

Cherin, M., Bertè, D.F., Rook, L. and Sardella, R. 2013a. Re-defining *Canis etruscus* (Canidae, Mammalia): A new look into evolutionary history of Early Pleistocene dogs resulting from the outstanding fossil record from Pantalla (Italy). *Journal of Mammalian Evolution*. DOI 10.1007/s10914-013-9227-4.

Cherin, M., Bertè, D.F., Sardella, R. and Rook, L. 2013b. *Canis etruscus* (Canidae, Mammalia) and its role in the faunal assemblage from Pantalla (Perugia, central Italy): comparison with the Late Villafranchian large carnivore guild of Italy. *Bollettino della Società Paleontologica Italiana.* **52(1)**, 11-18.

Christiansen, P. 1999. What size were *Arctodus simus* and *Ursus spelaeus* (Carnivora: Ursidae)? *Annales Zoologici Fennici*. **36**, 93-102.

Christiansen, P. and Wroe, S. 2007. Bite forces and evolutionary adaptations to feeding ecology in carnivores. *Ecology*. **88(2)**, 347-358.

Cohen, J.A. 1978. *Cuon alpinus*. *Mammalian Species.* **100**, 1-3.

Collinge, S.E. 2001. Body size and community structure in British Pleistocene mammals. Ph.D. Thesis. University College London, UK.

Conard, N. J. and Bolus, M. 2008. Radiocarbon dating the late Middle Paleolithic and the Aurignacian of the Swabian Jura. *Journal of Human Evolution.* **55**, 886-897.

Coope, G.R., Pennington, W., Mitchell, G.F., West, R.G., Morgan, A.V. and Peacock, J.D. 1977. Fossil Coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) Cold Stage [and Discussion]. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*. **280(972)**, 313-340.

Coope, G.R. 1979. Late Cenozoic fossil Coleoptera: evolution, biogeography and ecology. *Annual Review of Ecology and Systematics*. **10**, 247-267.

Coope, G.R., Gibbard, P.L., Hall, A.R., Preece, R.C., Robinson, J.E. and Sutcliffe, A.J. 1997. Climatic and environmental reconstructions based on fossil assemblages from Middle Devensian (Weichselian) deposits of the River Thames at South Kensington, central London, UK. Quaternary Science Reviews. **16**, 1163-1195.

Coope, G.R. 2001. Biostratigraphical distinction of interglacial coleopteran assemblages from southern Britain attributed to Oxygen Isotope Stages 5e-7. Quaternary Science Reviews. 20, 1717-1722.

Coope, G.R. 2010. Coleoptera from the Cromerian type site at West Runton, Norfolk, England. *Quaternary International*. 228, 46-52.

Cooper, S.M. 1990. The hunting behaviour of spotted hyaenas (*Crocuta crocuta*) in a region containing both sedentary and migratory populations of herbivores. *African Journal of Ecology*. **28(2)**, 131-141.

Corrunccini, R.S. 1975. Multivariate analysis in biological anthropology: some considerations. *Journal of Human Evolution.* **4**, 1-19.

Clift, W. 1823. A description of the fossil bones found in the caverns of Oreston referred to in the foregoing paper. In: Whidbey, J. 1823. On some fossil bones discovered in cavern in the lime-stone quarries of Oreston. *Philosophical Transactions of the Royal Society, London*. **113**, 81-90.

Clutton-Brock, T.H., Harvey, P.H. and Rudder, B. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature*. **269**, 797-800.

Clutton-Brock, T.H. and Albon, S.D. 1983. Climatic variation and body weight of Red deer. *The Journal of Wildlife Management*. **47(4)**, 1197-1201.

Clutton-Brock, J., Kitchener, A.C. and Lynch, J.M. 1994. Changes in the skull morphology of the Arctic wolf *Canis lupus arctos*, during the twentieth century. *Journal of Zoology, London.* **233**, 19-36.

Clutton Brock, J. 1995. Origins of the dog: domestication and early history. In: Serpell, J. (ed.) *The Domestic Dog, its evolution, behaviour and interactions with people*. Cambridge University Press. Pp 7-21

Collcutt, S.N., Currant, A.P. and Hawkes, C.J. 1981. A further report on the excavations at Sun Hole, Cheddar. *Proceedings of the University of Bristol Spelaeological Society*. **16(1)**, 21-38.

Creel, S. and Creel, N.M. 1996. Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*. **10(2)**, 526-538.

Crockford, S.J. and Kuzmin, Y.V. 2012. Comments on Germonpré et al., Journal of Archaeological Science. 36, 2009 "Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes", and Germonpré, Lázkičková-Galetová, and Sablin, Journal of Archaeological Science 39, 2012 "Palaeolithic dog skulls at the Gravettian Predmosti site, the Czech Republic". *Journal of Archaeological Science*. **39(8)**, 2797-2801.

Croitor, R. and Brugal, J-P. 2010. Ecological and evolutionary dynamics of the carnivore community in Europe during the last 3 million years. *Quaternary International*, 212, 98-108.

Currant, A. P. 1984. The Mammalian remains. In: Green, H. S. (ed.). *Pontnewydd Cave. A Lower Palaeolithic hominid site in Wales. The first report*. National Museum Wales Quaternary Studies Monograph **1**. 177-181.

Currant, A.P. 1987. Late Pleistocene Saiga antelope *Saiga tatarica* on Mendip. *Proceedings of the University of Bristol Spelaeological Society.* **18(1)**, 74-80.

Currant, A.P. 1998. Tornewton Cave. In: Campbell, S., Hunt, C. O., Scourse, J. D. & Keen, D. H. (eds.). *Quaternary of south-west England*. Geological Conservation Review Series. Chapman & Hall. 138-145.

Currant, A. and Jacobi, R. 2001. A formal mammalian biostratigraphy for the Late Pleistocene of Britain. *Quaternary Science Reviews*. **20**. 1707-1716.

Currant, A. 2004. The Quaternary mammal collections at the Somerset County Museum, Taunton. In: Schreve D. C (ed.). *The Quaternary Mammals of Southern and Eastern England. Field Guide* Quaternary Research Association. 101–109.

Currant, A. P. and Jacobi, R. M. 2011. The mammalian faunas of the British Late Pleistocene. In: Ashton, N. M., Lewis, S. G., Stringer, C. B. (Eds.). The Ancient Human Occupation of Britain. Dev. Quat. Sci. 14. Elsevier, pp. 165-180.

Cuzin, F. and Lenain, D.M. 2004. Ruppell's fox *Vulpes rueppellii*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 201-205.

Dalponte, J. and Courtenay, O. 2004. Hoary fox Pseudalopex vetulus. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 72-76.

Damuth, J. and MacFadden, B.J. 1990 Introduction: body size and its estimation. In: Damuth, J. and MacFadden, B.J. (eds.). *Body size in mammalian paleobiology: estimation and biological implications*. Cambridge University Press. Pp 1-10

Darwin, C. 1871. *The descent of man, and selection in relation to sex*. John Murray, London.

Davis, S. J. and Valla, F. R. 1978. Evidence for domestication of the dog 12,000 years ago in the Natufian of Israel. *Nature*. **276**, 608-610.

Davis, S. J. 1981. The effects of temperature change and domestication on the body size of Late Pleistocene to Holocene mammals of Israel. *Paleobiology*. **7(1)**, 101-114.

Davies, M. 1989. Recent advances in cave archaeology in southwest Wales. In: Ford, T. D. (ed.). *Limestones and caves of Wales*. Cambridge University Press. Pp 79-91.

Dawkins, W. B. 1867. On the age of the lower Brick-earths of the Thames Valley. *Quarterly Journal of the Geological Society*. **23**, 91-109.

Dawkins, W. B. 1874. *Cave Hunting: researches on the evidence of caves respecting the early inhabitants of Europe*. Wildhern Press (reprinted in 2009). Pp 455.

Dawkins, W. B. 1877. The exploration of the fossiliferous deposit at Windy Knoll, Castleton, Derbyshire. *Quarterly Journal of the Geological Society*. **33**, 724-729.

Dayan, T., Simberloff, D., Tchernov, E. and Yom-Tov, Y. 1992. Canine carnassials: character displacement in the wolves, jackals and foxes of Israel. *Biological Journal of the Linnean Society.* **45**, 315-331.

Dayan, T., Wool, D. and Simberloff, D. 2002. Variation and covariation of skulls and teeth: modern carnivores and the interpretation of fossil mammals. *Paleobiology*. **28(4)**, 508-526.

Dayan, T. and Simberloff, D. 2005. Ecological and community-wide character displacement: the next generation. *Ecology Letters*. **8(8)**, 875-894.

Daujeard, C., Fernandes, P., Guadelli, J-L., Moncel, M-H., Santagata, C. and Raynal, J-P. 2012. Neanderthals subsistence strategies in southeastern France between the plains of the Rhone Valley and the mid-mountains of the Massif Central (MIS 7 to MIS 3). *Quaternary International.* **252**, 32-47.

de Mello Beisiegel, B. and Zuercher, G.L. 2005. *Speothos venaticus. Mammalian Species*. **783**, 1-6.

Deguilloux, M. F., Moquel, J., Pemonge, M. H. and Colombeau, G. 2009. Ancient DNA supports lineage replacement in European dog gene pool; insight into Neolithic southeast France. *Journal of Archaeological Science*. **36**. 513-519.

Dietz, J.M. 1985. *Chrysocyon brachyurus. Mammalian Species*. **234**, 1-4.

Delgado Huertas, A., Iacumin, P. and Longinelli, A. 1997. A stable isotope study of fossil mammal remains from the Paglicci Cave, southern Italy, 13 to 33 ka BP: palaeoclimatological considerations. *Chemical Geology*. **141**, 211-223.

Dietrich, C. G. 2009. Steppe lion remains imported by Ice Age spotted hyaenas into the Late Pleistocene Perick Caves hyaena den in northern Germany. *Quaternary Research.* **71**,361-374.

Dijk, J. van, Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Brøseth, H., Andersen, R., Andersen, R., Steen, H. and Landa, A. 2008. Diet shift of a facultative scavenger, the wolverine, following recolonisation of wolves. *Journal of Animal Ecology*. **77**, 1183-1190.

Durbin, L.S., Venkataraman, A., Hedges, S. and Duckworth, W. 2004. Dhole *Cuon alpinus*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 210-219.

Duval, M., Falguères, C., Bahain, J. J., Grün, R., Shao, Q., Aubert, M., Hellstrom, J., Dolo, J-M., Agusti, J., Martinez-Navarro, B., Palmqvist, P. and Toro-Moyano, I. 2011. The challenge of dating Early Pleistocene fossil teeth by the combined uranium series–electron spin resonance method: the Venta Micena palaeontological site (Orce, Spain). *Journal of Quaternary Science*. **26(6)**, 603-615.

Ehlers, J. and Gibbard, P.L. 2007. The extent and chronology of Cenozoic Global Glaciation. *Quaternary International*. **164-165**, 6-20.

Eisenberg, J.F. 1990. The behavioural/ecological significance of body size in the Mammalia. In: Damuth, J. and MacFadden, B.J. (eds.) *Body size in mammalian paleobiology: estimation and biological implications.*Cambridge University Press. Pp 25-37.

Elgar, M.A. and Harvey, P.H. 1987. Basal metabolic rates in mammals: allometry, phylogeny and ecology. *Functional Ecology*. **1(1)**, 25-36.

Ewer, R.F. 1973. *The Carnivores*. Weidenfeld and Nicolson, London. Pp 494.

Fairbairn, D.J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics*. **28**. 659-687.

Finarelli, J. A. and Flynn, J. J. 2006. Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): the effects of incorporating data from the fossil record. *Systematic Biology*. **55(2)**, 301-313.

Finarelli, J. A. 2007. Mechanisms behind active trends in body size evolution of the Canidae (Carnivora: Mammalia). *The American Naturalist*. **170(6)**, 876-885.

Finarelli, J.A. 2008. Hierarchy and the reconstruction of evolutionary trends: evidence for constraints on the evolution of body size in terrestrial caniform carnivorans (Mammalian). *Paleobiology*. **34(4)**, 553-562.

Finlayson, C., Pacheco, F.G., Rodriguez-Vidal, J., Fa, D.A., Gutierrez Lopez, J.M., Perez, A.S., Finlayson, G., Allue, E., Preysler, J.B., Caceres, I., Carrion, J.S., Fernandez Jalvo, Y., Gleed-Owen, C.P., Jimenez Espejo, F.J., Lopez, P., Lopez Saez, J.A., Riquelme Cantal, J.A., Sanchez Marco, A., Giles Guzman, F., Brown, K., Fuentes, N., Valarino, C.A., Villalpando, A., Stringer, C.B., Martinez Ruiz, F. and Sakamoto, T. 2006. Late survival of Neanderthals at the southernmost extreme of Europe. *Nature*. **443**, 850-853.

Flagstad, Ø., Walker, C.W., Vilà, C., Sundqvist, A.-K., Fernholm, B., Hufthammer, A.K., Wiig, Ø., Koyola, I. and Ellegren, H. 2003. Two centuries of the Scandinavian wolf population: patterns of genetic variability and migration during an era of dramatic decline. *Molecular Biology*. **12**, 869-880.

Flynn, L. J., Tedford, R. H. And Qui, Z. 1991. Enrichment and stability in the Pliocene Mammalian Fauna of North China. *Paleobiology*. **17(3)**, 246-265.

Forsyth Major, C. J. 1890. Note on a Pliocene mammalian fauna at Olivola in the Upper Val di Magra (Prov. Massa-Carrara), Italy. *Geol. Mag.* **III (7)**. 305-308.

Forsten, A. 1993. Size decrease in Late Pleistocene-Holocene caballoid horses (Genus *Equus*), intra- or interspecific evolution? A discussion of alternatives. *Quaternary International*. **19**, 71-75.

Fortin, D., Beyer, H.L., Boyce, M.S. Smith, D.W., Duchesne, T. and Mao, J.S. 2005. Wolves influence elk movements: behaviour shapes a trophic cascase in Yellowstone National Park. *Ecology*. **86(5)**, 1320-1330.

Fritts, S. H., Mech, L. D. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildlife Monography*. **80**, 3-79.

Fritzell, E.K. and Haroldson, K.J. 1982. *Urocyon cinereoargenteus. Mammalian Species*. **189**, 1-8.

Fuller, T.K. and Cypher, B.L. 2004. Gray fox *Urocyon cinereoargenteus*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 92-97.

Funnell, B.M. 1995. Global sea-level and the (pen-)insularity of late Cenozioc Britain. In: Preece, R.C. (ed.) *Island Britain: a Quaternary perspective*. Geological Society Special Publication, **96**, 3-13.

Garcia, N. and Arsuaga, J.L. 1999. Carnivores from the Early Pleistocene hominid-bearing Trinchera Dolina 6 (Sierra de Atapuerca, Spain). *Journal of Human Evolution.* **37**, 415-430.

Garcia, N. and Virgos, E. 2007. Evolution of community composition in several carnivore palaeoguilds from the European Pleistocene: the role of interspecific competition. *Lethaia*. **40**, 33-44.

Garland, T. Jr. 1983a. Scaling the ecological cost of transport to body mass in terrestrial mammals. *The American Naturalist*. **121(4)**, 571-587.

Garland, T. Jr. 1983b. The relation between maximal running speed and body mass in terrestrial mammals. *Journal of Zoology, London*. **199**, 157-170

Garland, T. Jr. and Janis, C.M. 1993. Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? *Journal of Zoology, London.* **229**, 133-151.

Garrido, G. and Arribas, A. 2008. *Canis accitanus* nov. sp., a new small dog (Canidae, Carnivora, Mammalia) from the Fonelas P-1 Plio-Pleistocene site (Guadix basin, Granada, Spain). *Geobios*. **41**, 751-761.

Gascoyne, M., Currant, A. P. and Lord, T. C. 1981. Ipswichian fauna of Victoria Cave and the marine palaeoclimatic record. *Nature*. **294**, 652-654.

Gaubert, P., Bloch, C., Benyacoub, S., Abdelhamid, A., Pagani, P., Adeyemi, C., Sylvestre Djagoun, M., Couloux, A., Dufour, S. 2012. Reviving the African wolf *Canis lupus lupaster* in North and West Africa: a mitochondrial lineage ranging more than 6,000Km wide. *PLOS one.* **7(8)**, 1-10.

Gaudzinski, S. 2000. On the variability of Middle Palaeolithic procurement tactics: the case of Salzgitter Lebenstedt, northern Germany. *International Journal of Osteoarchaeology.* **10**, 396-406.

Gaudzinski, S. and Roebroeks, W. 2000. Adults only. Reindeer hunting at the Middle Palaeolithic site Salzgitter Lebenstedt, northern Germany. *Journal of Human Evolution*. **38**, 497-521.

Geffen, E., Gompper, M.E., Gittleman, J.L., Luh, H-K., MacDonald, D.W. and Wayne, R.K. 1996. Size, life-history traits and social organisation in the Canidae: a reevaluation. *The American Naturalist.* **147(1)**, 140-160.

Germonpré, M., Sablin, M. V., Stevens, R. E., Hedges, R. E. M., Hofreiter, M., Stiller, M. and Despres, V. R. 2009. Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes. *Journal of Archaeological Science.* **36**, 473-490.

Gese, E.M. and Bekoff, M. 2004. Coyote *Canis latrans.* In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 81-87.

Gese, E.M., Bekoff, M., Andelt,W., Carbyn, L. and Knowlton, F. 2008. *Canis latrans*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Downloaded on **27 August 2013**.

Ghezzo, E., Berté, D. F. and Sala, B.2013. The revaluation of Galerian Canidae, Felidae and Mustelidae of the Cerè Cave (Verona, northeastern Italy). *Quaternary International*. ://dx.doi.org/10.1016/j.quaint.2012.12.031.

Gibbard, P. L. and Stuart, A. J. 1975. Flora and vertebrate fauna of the Barrington Beds. *Geol. Mag*. **112 (5).** 493-501.

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. and Charnov, E. L. 2001. Effects of size and temperature on metabolic rate. *Science*. **293(5538)**, 2248-2251.

Gilmour, M., Currant, A., Jacobi, R. and Stringer, C. 2007. Recent TIMS dating results from British Late Pleistocene vertebrate faunal localities: context and interpretation. *Journal of Quaternary Science*. **22(8)**, 793-800.

Gingerich, P.D. and Winkler, D.A. 1979. Patterns of variation and correlation in the dentition of the red fox, *Vulpes vulpes*. *Journal of Mammalogy*. **60(4)**, 691-704.

Gittleman, J.L. and Harvey, P.H. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioural Ecology and Sociobiology*. **10(1)**, 57-63.

Gittleman, J.L. 1985. Carnivore body size: Ecological and taxonomic correlates. *Oecologia*. **67**. Pp 540-554.

Gittleman, J.L. 1986. Carnivore life history patterns: allometric, phylogenetic, and ecological associations. *The American Naturalist*. **127(6)**, 744-771.

Gittleman, J.L. and Van Valkenburgh, B. 1997. Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology. *Journal of Zoology, London*. **242**, 97-117.

Gliozzi, E., Abbazzi, L., Argenti, A., Azzaroli, A., Caloi, L., Capasso Barbato, L., di Stefano, G., Esu, D., Ficcarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M. R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanalda, E. And Torre, D. 1997. Biochronology of selected Mammals. Molluscs and Ostracodes from tyhe Middle Pliocene to the Late Pleistocene in Italy. The state of the art. *Rivista Italiana di Paleontologia e Stratigrafia*. **103(3)**, 369-388.

Gompper, M.E. 2002. Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of northeastern North America by coyotes. *BioScience*. **52(2)**, 185-190.

Gonzalez del Solar, R. and Rau, J. 2004. Chilla *Pseudalopex griseus*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 56-63.

Green, H. S., Stringer, C. B., Collcutt, S. N., Currant, A. P., Huxtable, J., Schwarcz, H. P., Debenham, N., Embleton, C., Bull, P., Molleson, T. I. and Bevins, R. E. 1981. Pontnewydd Cave in Wales - a new Middle Pleistocene hominid site. *Nature*. **294**. 707-713.

Green, C.P., Coope, G.R., Currant, A.P., Holyoak, D.T., Ivanovich, M., Jones, R.L., Keen, D.H., McGregor, D.F.M. and Robinson, J.E. 1984. Evidence of two temperate episodes in late Pleistocene deposits at Marsworth. *Nature.* 309, 778-781.

Guilday, J.E. 1962. Supernumerary molars of *Otocyon*. *Journal of Mammalogy*. **43 (4)**, 455-462.

Haas, S.K., Hayssen, V. and Krausman, P.R. 2005. *Panthera leo*. *Mammalian Species*. **762**, 1-11.

Haltenorth, T. and Roth, H. H. 1968. Short review of the biology and ecology of the red fox. *Saugetierkunde Mitteilungen*. **16**, 339-352.

Hamblin, R.J.O., Moorlock, B.S.P., Rose, J., Lee, J.R., Riding, J.B., Booth, S.J. and Pawley, S.M. 2005. Revised pre-Devensian glacial stratigraphy in Norfolk, England, based on mapping and till provenance. *Netherlands Journal of Geosciences*. **84(2)**, 77-85.

Harrison, R.A. 1977. The Uphill Quarry Caves, Weston-super-Mare, a reappraisal. *Proceedings of the University of Bristol. Spelaeological Society*. **14(3)**, 233-254.

Hartstone-Rose, A., Werdelin, L., De Ruiter, D.J., Berger, L.R. and Churchill, S.E. (2010). The Plio-Pleistocene ancestor of wild dogs, *Lycaon sekowei* n. sp. *Journal of Paleontology*. **84(2)**, 299-308.

Hattingh, I. 1956. Measurements of foxes from Scotland and England. *Proceedings of the Zoological Society, London*. **127(2)**, 191-199.

Hawkins, D. 2009. Biomeasurement a student's guide to biological statistics. Oxford University Press, Oxford, UK. Pp 333.

Hayes, J.P. and Garland, T.Jr. 1995. The evolution of endothermy: testing the aerobic capacity model. *Evolution*. **49(5)**, 836-847.

Haynes, G. 1982. Utilization and skeletal disturbances of North American prey carcasses. *Arctic*. **35(2)**, 266-281.

Hayssen, V. and Lacy, R.C. 1985. Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comparative Biochemistry and Physiology Part A: Physiology*. **81(4)**, 741-754.

Hayward, M.W. 2006. Prey preferences of the spotted hyaena (*Crocuta crocura*) and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology*. **270**, 606-614.

Hefner, R. and Geffen, E. Group size and home range of the Arabian wolf (*Canis lupus*) in southern Israel. *Journal of Mammalogy*. **80(2)**, 611-619.

Hemmer, H. 2002. Die Feliden aus dem Epivillafranchium von Untermassfeld. In: Kahlke, R-D. (ed.). *Das Pleistozän von Untermassfeld Bei Meiningen (Thuringen)*. Römisch-Germanisches Zentralmuseum Bande. **40(3)**, 699–782.

Hemmer, H., Kahlke, R. D. and Vekua, A. K. 2004. The Old World puma-Puma pardoides (Owen, 1846)(Carnivora: Felidae)-in the Lower Villafranchian (Upper Pliocene) of Kvabebi (East Georgia, Transcaucasia) and its evolutionary and biogeographical significance. *Neues Jahrbuch fur Geologie und Paläontologie-Abhandlungen*. **233(2)**, 197-231.

Hemmer, H., Kahlke, R-D. and Vekua, A.K. 2011. The cheetah *Acinonyx pardinensis* (Croizet et Jobert, 1828) s.l. at the hominin site of Dmanisi (Georgia) – A potential prime meat supplier in Early Pleistocene ecosystems. *Quaternary Science Reviews.* **30**, 2708-2714.

Hersteinsson, P. and Macdonald, D.W. 1992. Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos*. **64(3)**, 505-515.

Higham, T., Compton, T., Stringer, C., Jacobi, R., Shapiro, B., Trinkaus, E., Chandler, B., Groning, F., Collins, C., Hillson, S., O'Higgins, P., FitzGerald, C. and Fagan, M. 2011. The earliest evidence for anatomically modern humans in northwestern Europe. *Nature*. **479(7374)**, 521-524.

Hildebrand, M. 1952. An analysis of the body proportions in the Canidae. *American Journal of Anatomy*. **90**, 217-256.

Hillson, S. 2005. *Teeth.* Cambridge University Press. Pp 373.

Hoare, P.G., Gale, S.J., Robinson, R.A.J., Connell, E.R. and Larkin, N.R. Marine Isotope Stage 7-6 transition age for beach sediments at Morston, north Norfolk, UK: implications for Pleistocene chronology, stratigraphy and tectonics. *Journal of Quaternary Science*. **24(4)**, 311-316.

Hone, D.W.E. and Benton, M.J. 2005. The evolution of large size: how does Cope's Rule work? *Trends in Ecology and Evolution*. **20(1),** 4-6.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*. **93(870)**, 145-159.

Iacumin, P., Bocherens, H., Delgado Huertas, A., Mariotti, A. and Longinelli, A. 1997. A stable isotope study of fossil mammal remains from the Paglicci Cave, Southern Italy. N and C as palaeoenvironmental indicators. *Earth and Planetary Science Letters.* **148**, 349-357.

Isaac, J.L. 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mammal Review*. **35(1)**, 101-115.

Iurino, D.A., Fico, R., Petrucci, M. and Sardella, R. 2013. A pathological Late Pleistocene canid from San Sidero (Italy): implications for social- and feeding-behaviour. *Naturwissenschaften*. DOI 10.1007/s00114-013-1018-5.

Jablonski, D. 1997. Body-size evolution in Cretaceous molluscs and the status of Cope's rule. *Nature*. **385(16)**, 250-252.

Jacobi, R. M., Rowe, P. J., Gilmour, M. A., Grün, R. and Atkinson, T. C. 1998. Radiometric dating of the Middle Palaeolithic tool industry and associated fauna of Pin Hole Cave, Creswell Crags, England. *Journal of Quaternary Science.* **13(1),** 29-42.

Jacobi, R.M. 2000. The Late Pleistocene archaeology of Somerset. In: Webster, C.J. (Ed.), *Somerset Archaeology*. Papers to Mark 150 Years of the Somerset Archaeological and Natural History Society. Somerset County Council, Taunton. pp 45-52.

Jacobi, R. M. and Higham, T. F. G. 2008. The 'Red Lady' ages gracefully: new ultrafiltration AMS determinations from Paviland. *Journal of Human Evolution*. **55**, 898-907.

Jacobi, R.M., Rose, J., MacLeod, A. and Higham, T.F.G. 2009. Revised radiocarbon ages on woolly rhinoceros (*Coelodonta antiquitatis*) from western central Scotland: significance for timing the extinction of woolly rhinoceros in Britain and the onset of the LGM in central Scotland. *Quaternary Science Reviews*. **28**, 2551-2556.

Janis, C.M. and Wilhelm, P.B. 1993. Were there mammalian pursuit predators in the Tertiary? Dances with wolf avatars. *Journal of Mammalian Evolution*. **1(2)**, 103-125.

Jędrzejewski, W., Jędrzejewska, B., Okarma, H., Schmidt, K., Bunevich, A. N. and Milkowski, L. 1996. Population dynamics (1869–1994), demography, and home ranges of the lynx in Bialowieza Primeval Forest (Poland and Belarus). *Ecography*. **19(2)**, 122-138.

Jędrzejewski, W., Jędrzejewska, B., Okarma, H., Schmidt, K., Zub, K., Musiani, M. 2000. Prey selection and predation by wolves in Białowieza Primeval Forest, Poland. *Journal of Mammalogy*. **81(1)**, 197-212.

Jhala, Y.V. and Moehlman, P.D. 2004, Golden jackal *Canis aureus*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 156-161.

Jimenez, J.E. and Novaro, A.J. 2004. Culpeo *Pseudalopex culpaeus*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 44-49.

Johnsingh, A.J.T. and Jhala, Y.V. 2004. Indian fox *Vulpes bengalensis*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 219-222.

Kahlke, H-D. 1977. *Das Pleistozän von Taubach bei Weimar*. Akademie Verlag, Berlin.

Kahlke, R.-D., 1999. The History of the Origin, Evolution and Dispersal of the Late Pleistocene Mammuthus-Coelodonta Faunal Complex in Eurasia (Large Mammals). Fenske Companies, Rapid City.

Kahlke, R-D. 2000. The Early Pleistocene (Epivillafranchian) faunal site of Untermassfeld (Thuringia, Central Germany) synthesis of new results. *Eraul*. **92**, 123-138.

Kahlke, R-D. 2002. The Quaternary large mammal faunas of Thuringia (Central Germany). In: Meyrick, R.A. and Schreve, D.C. *The Quaternary of Central Germany. Field Guide*. Quaternary Research Association, London. 59-78.

Kahlke, R-D. and Gaudzinski, S. 2005. The blessing of a great flood: differentiation of mortality patterns in the large mammal record of the Lower Pleistocene fluvial site of Untermassfeld (Germany) and its relevance for the interpretation of faunal assemblages from archaeological sites. *Journal of Archaeological Science.* **32(8)**. 1202-1222.

Kahlke, R-D., Garcia, N., Kostopoulos, D. S., Lacombat, F., Lister, A. M., Mazza, P. P. A., Spassov, N., Titov, V. V. 2011. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. *Quaternary Science Reviews*. **30**, 1368-1395.

Karanth, K. U. and Sunquist, M. E. 1995. Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology*. **64(4)**, 439-450.

Kays, R., Curtis, A. and Kirchman, J.J. 2010. Rapid adaptive evolution of northeastern coyotes via hybridisation with wolves. *Biology Letters*. **6(1)**, 89-93.

Keen, D.H. 1995. Raised beaches and sea-levels in the English Channel in the Middle and Late Pleistocene: problems of interpretation and implications for the isolation of the British Isles. In: Preece, R.C. (ed.) *Island Britain: a Quaternary perspective*. Geological Society Special Publication, **96**, 63-74.

Keen, D. H. 1998. Kent's Cavern. In Campbell, S., Hunt, C. O., Scourse, J. D. and Keen, D. H. (eds.). *Quaternary of south-west England*. Geological Conservation Review Series. Chapman & Hall. Pp 134-138.

Keiser, J.A. 1995. Gnathomandibular morphology and character displacement in the Bat-eared fox. *Journal of Mammalogy*, **76(2)**, 542-550.

Kennard, A.S. 1944. The Crayford Brickearths. *Proceedings of the Geologists Association*. **55 (3)**, 121-169.

Kerney, M.P., Gibbard, P.L., Hall, A.R. and Robinson, J.E. 1982. Middle Devensian river deposits beneath the 'Upper Floodplain' terrace of the River Thames at Isleworth, West London. *Proceedings of the Geologists Association.* **93(4)**, 385-393.

Kingdon, J. 1977. East African Mammals: Volume IIIA, Carnivores. Academic Press, London.

Kojola, I., Huitu, O., Toppinen, K., Heikura, K., Heikkinen, S., Ronkainen, S. 2004. Predation on European wild forest reindeer (*Rangifer tarrandus*) by wolves (*Canis lupus*) in Finland. *Journal of Zoology*. **263**, 229-235.

Kolfschoten, T. van. 2000. The Eemian mammalian fauna of Europe. *Netherlands Journal of Geosciences*. **79(2/3)**, 269-281.

Kleiber, M. 1932. Body size and metabolism. *Hilgardia*. **6(11)**, 315-353.

Kruuk, H. and Turner, M. 1967. Comparative notes on predation by lion, leopard, cheetaj and wild dog in the Serengeti area, east Africa. *Mammalia*. **31(1)**, 1-23.

Kruuk, H. 1972. The spotted hyena. A study of predation and social behaviour. The University of Chicago Press, Chicago.

Kunkel, K.E., Ruth, T.K., Pletscher, D.H. and Hornocker, M.G. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park Montana. *The Journal and Wildlife Management*. **63(3)**, 901-910.

Kurtén, B. 1968. *Pleistocene Mammals of Europe*. Weidenfeld and Nicholson, London. Pp 317.

Kurtén, B. 1974. A history of coyote-like dogs (Canidae, Mammalia). *Acta Zoologica Fennica*. Separatum. **140**, 1-38.

Kurtén, B. and Poulianos, A.N. 1977. New stratigraphic and faunal material from Petralona Cave with special reference to the carnivora. *Anthropos*. **4(1-2)**, 47-130

Kurtén, B. 1978. The lynx from Etouaires, *Lynx issiodorensis* (Croziet & Jobert), late Pliocene. *Annales Zoologici Fennici*. **15**, 314-322.

Kurtén, B. and Poulianos, A.N. 1981. Fossil Carnivora of Petralona Cave: status of 1980. *Anthropos.* **8**, 9-56.

Lacombat, F., Abbazzi, L., Ferretti, M.P., Martinez-Navarro, B., Moulle, P-E, Palombo, M-R., Rook, L., Turner, A. And Valli, A. M-F. 2008. New data on the early Villafranchian fauna from Vialette (Haute-Loire, France) based on the collection of the Crozatier Museum (Le Puy-en-Velay, Haute-Loire, France). *Quaternary International*. **179**, 64-71.

Lambeck, K. 1995. Late Devensian and Holocene shorelines of the British Isles and North Sea from models of glacio-hydro-isostatic rebound. *Journal of the Geological Society, London.* **152**, 437-448.

Lambert, F., Delmonte, B., Petit, J.R., Bigler, M., Kaufmann, P.R., Hutterli, M.A., Stocker, T.F., Ruth, U., Steffensen, J.P. and Maggi, V. 2008. Dust-climate couplings over the past 800,000 years from the EPICA Dome C ice core. *Nature*. **452**, 616-619.

Landa, A., Strand, O., Swenson, J. E., and Skogland, T. 1997. Wolverines and their prey in southern Norway. *Canadian Journal of Zoology*. **75(8)**, 1292-1299.

Larson, G., Karlsson, E.K., Perri, A., Webster, M.T., Ho, S.Y.W., Peters, J., Stahl, P.W., Piper, P.J., Lingaas, F., Fredholm, M., Comstock, K.E., Modiano, J.F., Schelling, C., Agoulnik, A.I., Leegwater, P.A., Dobney, K., Vigne, J-D., Vila, C., Andersson, L. and Lindblad-Toh, K. 2012. Rethinking dog domestication by integrating genetics, archaeology, and biogeography. *PNAS*. **109(23)**, 8878-8883.

Legendre, S. and Roth, C. 1988. Correlation of carnassial tooth size and body weight in recent carnivores (Mammalia). *Historical Biology*. **1**, 85-98.

Leonard, J. A., Vilà, C., Fox-Dobbs, K., Koch, P. L., Wayne, R. K., Van Valkenburgh, B. 2007. Megafaunal extinctions and the disappearance of a specialised wolf ecomorph. *Current Biology*. **17**, 1146-1150.

Leon-Velarde, F., Muizon, C. de, Palacios, J.A., Clark, D. and Monge-C, C. 1996. Hemoglobin affinity and structure in high-altitude and sea-level carnivores from Peru. *Comparative Biochemistry and Physiology.* **113A(4)**, 407-411.

Lewis, M., Pacher, M., Turner, A. 2010. The larger Carnivora of the West Runton Freshwater Bed. *Quaternary International*. **228(1)**, 116-135.

Lindenfors, P., Gittleman, J.L. and Jones, K.E. 2007. Sexual size dimorphism in mammals. In: Fairbairn, D.J., Blackenhorn, W.U. and Szekely, T. (eds.) *Sex, size and gender roles. Evolutionary studies of sexual size dimorphism*. Oxford University Press, Oxford. Pp 16-26.

Linnel, J.D.C., Andersen, R., Kvam, T., Andren, H., Liberg, O., Odden, J., Moa, P.F. 2001. Home range size and choice of management strategy for Lynx in Scandinavia. *Environmental Management*. **27(6)**, 869-879.

Linnel, J.D.C., Andersen, R., Andersone, Z., Balciauskas, L., Blanco, J.C., Boitani, L., Brainerd, S., Breitenmoser, U., Kojala, I., Liberg, O., Løe, J., Okarma, H., Pedersen, H.C., Promberger, C., Sand, K., Solberg, E.J., Valdmann, H. and Wabakken, P. 2002. The fear of wolves: a review of wolf attacks on humans. *NINA Oppdragsmelding*. **731**, 1-65.

Lisiecki, L.E. and Raymo, M.E. 2007. Plio-Pleistocene climate evolution: trends and transitions in glacial cycle dynamics. *Quaternary Science Reviews*. **26**, 56-69.

List, R. and Cypher, B.L. 2004. Kit fox *Vulpes macrotis*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 105-109.

Losey, R. J., Bazaliiskii, V. I., Garvie-Lok, S., Germonpré, M., Leonard, J. A., Allen, A. L., Katzenberg, M. A. and Sablin, M. V. 2011. Canids as persons: Early Neolithic dog and wolf burials, Cis-Baikal, Siberia. *Journal of Anthropological Archaeology*. **30(2)**, 174-189.

Lovegrove, B.G. 2000. The zoogeography of mammalian basal metabolic rate. *The American Naturalist.* **156(2)**, 201-219.

Loveridge, A.J. and Nel, J.A.J. 2004. Black-backed jackal *Canis mesomelas*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 161-166.

Lucherini, M., Pessino, M. and Farias, A.A. 2004. Pampas fox *Pseudalopex gymnocerus*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 63-68.

Lumley, H., De, Kahlke, H.-D., Moignem, A.-M. and Moullém, P.-E., 1988. Les faunes de grands Mammiféres de La Grotte du Vallonnet Roquebrune-Cap Martin, Alpes-Maritimes. *L'Anthropologie*. **92**, 465–495.

Macdonald, D. W. 1983. The ecology of carnivore social behaviour. *Nature*. **301**, 379-384.

Macdonald, D. W. 2009. *The Encyclopedia of Mammals*. Oxford University Press. Pp 936.

Maddy, D., Lewis, S.G., Scaife, R.G., Bowen, D.Q., Coope, G.R., Green, C.P., Hardaker, T., Keen, D.H., Rees-Jones, J., Parfitt, S. and Scott, K. 1998. The Upper Pleistocene deposits at Cassington, near Oxford, England. *Journal of Quaternary Science*. **13(3)**, 205-231.

Manning, A.D., Gordon, I.J. and Ripple, W.J. 2009. Restoring landscapes of fear with wolves in the Scottish Highlands. *Biological Conservation*. **142**, 2314-2321.

Marti, C.D., Steenhof, K., Kochert, M.N. and Marks, J.S. 1993. Community trophic structure: the roles of diet, body size and activity time in vertebrate predators. *Oikos*. **67(1)**, 6-18.

Martinez-Navarro, B. and Rook, L. 2003. Gradual evolution in the African Hunting dog lineage systematic implications. *Comptes Rendus Palevol*. **2**, 695-702.

Martinez-Navarro, B., Belmaker, M. and Bar-Yosef, O. 2009. The large carnivores from 'Ubeidiya (early Pleistocene, Israel): biochronological and biogeographical implications. *Journal of Human Evolution*. **56(5)**, 514-524.

Maul L. C. and Parfitt, S. A. 2010. Micromammals from the 1995 Mammoth Excavation at West Runton, Norfolk, UK: Morphometric data, biostratigraphy and taxonomic reappraisal. *Quaternary International*. **228**, 91-115.

Masini, F. and Torre, D. 1990. Large Mammal Dispersal Events at the Beginning of the Late Villafranchian. In: Lindsay, E. H., Fahlbusch, V. and Mein, P. (eds.) *European Neogene mammal chronology.* Nato ASI series A: Life Sciences. Plenum Press, New York. Pp 131-138.

Masini, F. and Sala, B. 2007. Large- and small- mammal distribution patterns and chronostratigraphic boundaries from the Late Pliocene to the Middle Pleistocene of the Italian peninsula. *Quaternary International*. **160**, 43-56.

Maslin, M.A., Seidov, D., Lowe, J. 2001. Synthesis of the nature and causes of sudden climate transitions during the Quaternary In: Seidov, D. Haupt B. & Maslin, M.A. (eds). *The Oceans and Rapid Climate Change: Past, Present and Future*. AGU Geophysical Monograph Series. **126**, 9-52.

Martinson, D.G., Pisias, N.G., Hays, J.D., Imbrie, J., Moore, T.C. Jr. and Shackleton, N.J. 1987. Age dating and the oribital theory of the Ice Ages: development of a high-resolution 0 to 300,000 year Chronostratigraphy. *Quaternary Research.* **27**, 1-29.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, U.S.A.

McFarlane, D.A. and Lundberg, J. 2013. On the occurrence of the scimitar-toothed cat, *Homotherium latidens* (Carnivora; Felidae), at Kents Cavern, England. *Journal of Archaeological Science.* **40**, 1629-1635.

McLellan, B.N., Servheen, C. and Huber, D. (IUCN SSC Bear Specialist Group) 2008. *Ursus arctos*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Downloaded on **27 August 2013**.

McNab, B.K. 1970. Body weight and the energetic of temperature regulation. *Journal of Experimental Biology*. **53**. 329-348.

McNab, B.K. 1971. On the ecological significance of Bergmann's rule. *Ecology*. **52(5)**, 845-854.

McNab, B.K. 1980. Food habits, energetics and the population biology of mammals. *The American Naturalist*. **116(1)**, 106-124.

McNab, B.K. 1988. Complications inherent in scaling the basal rate of metabolism in mammals. *The Quaterly Review of Biology*. **63(1)**, 25-54.

McNab, B.K. 1990. The physiological significance of body size. In: Damuth, J. and MacFadden, B.J. (eds.) *Body size in mammalian paleobiology: estimation and biological implications.*Cambridge University Press. Pp 11-23.

McNab, B.K. 1997. On the utility of uniformity in the definition of basal rate of metabolism. *Physiological Zoology*. **70(6)**, 718-720.

Meachen-Samuels, J. and Van Valkenburgh, B. 2009. Craniodental indicators of prey size preference in the Felidae. *Biological Journal of the Linnean Society.* **96**, 784-799.

Mech, L.D. 1970. *The wolf: the ecology and behaviour of an endangered species*. The American Museum of Natural History. The Natural History Press, New York. Pp 384.

Mech, L. D., Frenzel, Jr, L. D. and Karns, P. D. 1971. The effect of snow conditions on the vulnerability of white-tailed deer to wolf predation. In: Mech, L. D., Frenzel, Jr, L. D. (Eds.) *Ecological studies of the timber wolf in northeastern Minnesota*. Forest Service: U.S. Department of Agriculture, pp. 51-59.

Mech, L.D. 1974. *Canis lupus. Mammalian Species*. **37**, 1-6.

Mech, L.D. and Korb, M. 1978. An unusually long pursuit of a deer by a wolf. *Journal of Mammalogy*. **59(4)**, 860-861.

Mech, L. D. and Boitani, L. (IUCN SSC Wolf Specialist Group) 2010. *Canis lupus*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. <www.iucnredlist.org>. Downloaded on **03 April 2013**.

Meiri, S. and Dayan, T. 2003. On the validity of Bergmann's rule. *Journal of Biogeography*. **30**, 331-351.

Meiri, S., Dayan, T. and Simberloff, D. 2005. Variability and correlations in carnivore crania and dentition. *Functional Ecology*. **19**, 337-343.

Meloro, C., Raia, P. and Barbera, C. 2007. Effect of predation on prey abundance and survival in Plio-Pleistocene mammalian communities. *Evolutionary Ecology Research*. **9**, 505-525.

Meloro, C., Elton, S., Louys, J., Bishop, L.C. and Ditchfield, P. 2013. Cats in the forest: predicting habitat adaptations from humerus morphometry in extant and fossil Felidae (Carnivora). *Paleobiology*. **39(3)**, 323-344.

Mendoza, M., Janis, C.M. and Palmqvist, P. 2006. Estimating the body mass of extinct ungulates: a study on the use of multiple regression. *Journal of Zoology*. **270**, 90-101.

Meriggi, A. and Lovari, S. 1996. A review of wolf predation in southern Europe: Does the wolf prefer wild prey to livestock? *Journal of Applied Ecology*. **33(6)**, 1561-1571.

Montoya, P., Morales, J. and Abella, J. 2009. *Eucyon debonisi* n. Sp., a new Canidae (Mammalia, Carnivora) from the latest Miocene of Venta del Moro (Valencia, Spain). *Geodiversitas*. **31(4)**, 709-722.

Montuire, S. and Marcolini, F. 2002. Palaeoenvironmental significance of the mammalian faunas of Italy since the Pliocene. *J. Quat. Sci.* **17 (1)**. 87-96.

Mosimann, J.E. and Frances, C.J. 1979. New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution.* **33(1)**, 444-459.

Muller-Beck, H. and Workman, K. 1968. A possible source for the Vogelherd Aurignacian. *Arctic Anthropology*. **5(1)**, 48-61.

Müller, U.C., Pross, J. and Bibus, E. 2003. Vegetation response to rapid climate change in Central Europe during the past 140,000 yr based on evidence from the Füramoos pollen record. *Quaternary Research*. **59**, 235-245.

Munzel, S.C. and Conard, N.J. 2004. Change and continuity in subsistence during the Middle and Upper Palaeolithic in the Ach Valley of Swabia (south-west Germany). *International Journal of Osteoarchaeology*. **14**, 225-243.

Munzel, S.C., Stiller, M., Hofreiter, M., Mittnik, A., Conard, N.J. and Bocherens, H. 2011. Pleistocene bears in the Swabian Jura (Germany): Genetic replacement, ecological displacement, extinctions and survival. *Quaternary International.* **245(2)**, 225-237.

Murton, J. B., Baker, A., Bowen, D. Q., Caseldine, C. J., Coope, G. R., Currant, A. P., Evans, J. G., Field, M. H., Green, C. P., Hatton, J., Ito, M., Jones, R. L., Keen, D. H., Kerney, M. P., McEwen, R., McGregor, D. F. M., Parish, D., Robinson, J. E., Schreve, D. C. and Smart, P. L. 2001. A late Middle Pleistocene temperate-periglacial-temperate sequence (Oxygen Isotope Stages 7-5e) near Marswoth, Buckinghamshire, UK. *Quaternary Science Reviews*. **20**, 1787-1825.

Nagy, K.A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs*. **57(2)**, 111-128.

Napoleone, G., Albianelli, A., Azzaroli, A., Bertini, A., Magi, M. and Mazzini, M. 2003. Calibration of the Upper Valdarno Basin to the Plio-Pleistocene for correlating the Apennine continental sequences. *Il Quaternario*. **16**, 131-166.

Naughton-Treves. L., Grossberg, R. and Treves, A. 2003. Paying for tolerance: rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology*. **17(6)**, 1500-1511.

Nedervelde, J. van, Davies, M. and John, B.S. 1973. Radiocarbon dating from Ogof yr Ychen, a new Pleistocene site in west Wales. *Nature*. **245**, 453-454.

Nel, J.A.J. and Maas, B. 2004. Bat-eared fox *Otocyon megalotis*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 183-189.

Nowak, R. 1991. Walker's Mammals of the World. Baltimore: Johns Hopkins University Press.

Nowak, R.M. 1999. Walker's Mammals of the World Volume 1. Johns Hopkins University Press, U.S.A. Sixth edition.

Nowak, S., Mysłajek, R. W., Kłosińska, A., Gabryś, G. 2011. Diet and prey selection of wolves (*Canis lupus*) recolonising Western and Central Poland. *Mammalian Biology*. **76**, 709-715.

Ohmert, W. 1988. *Geologishe karte 1:25000 von Baden-Württemberg*. Geologischen Landesamt Baden-Württemberg. Stuttgart.

O'Regan, H.J., Turner, A. and Wilkinson, D.M. 2002. European Quaternary refugia: a factor in large carnivore extinction? *Journal of Quaternary Science*, **17(8)**, 789-795.

O'Regan, H.J. and Kitchener, A. 2005. The effects of captivity on the morphology of captive, domesticated and feral mammals. *Mammal Review*. **35**, 215-230.

Ovodov, N.D., Crockford, S.J., Kuzmin, Y.V., Higham, T.F.G., Hodgins, G.W.L. and van der Plicht, J. 2011. A 33,000 year old incipient dog from the Altai Mountains of Siberia: evidence of the earliest domestication disrupted by the Last Glacial Maximum. *PLoS one*. **6(7)**, 1-7.

Palombo, M.R., Milli, S. and Rosa. C. 2003-2004. Remarks on the biochronology of the late Middle Pleistocene mammalian faunal complexes of the Campagna Romana (Latium, Italy). *Geologica Romana*. **37**, 135-143.

Palmobo, M.R. and Valli, A.M.F. 2003-2004. Remarks on the biochronology of mammalian faunal complexes from the Pliocene to the Middle Pleistocene in France. Geologica Romana. 37, 145-163.

Palmqvist, P., Arribas, A. and Martinez-Navarro, B. 1999. Ecomorphological study of large canids from the lower Pleistocene of southeastern Spain. *Lethaia*. **32**, 75-88.

Palmqvist, P., Mendoza, M., Arribas, A., and Grocke, D. R. 2002. Estimating the body mass of Pleistocene canids: discussion of some methodological problems and a new 'taxon free' approach. *Lethaia*, **35(4)**, 358-360.

Palmqvist, P., Grocke, D.R., Arribas, A. and Farina, R.A. 2003. Paleoecological reconstruction of a lower Pleistocene large mammal community using biogeochemical ($\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, Sr:Zn) and ecomorphological approaches. *Paleobiology.* **29(2)**, 205-229.

Palmqvist, P., Perez-Claros, J.A., Janis, C. M. and Grocke, D.R. 2008. Tracing the ecophysiology of ungulates and predator-prey relationships in an early Pleistocene large mammal community. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **266**, 95-111.

Palmqvist, P., Martinez-Navarro, B., Perez-Claros, J.A., Torregrosa, V., Figueirido, Jimenez-Arenas, J.M., Patrocinio Espigares, M., Ros-Montoya, S. and De Renzi, M. 2011. The giant hyaena *Pachycrocuta brevirostris*: modelling the bone-cracking behaviour of an extinct carnivore. *Quaternary International*. 243(1), 61-79.

Paquet, P. C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. *Journal of Mammalogy*. **73(2)**, 337-343.

Parfitt, S. A. 1999. Mammalia. In Roberts, M. B. and Parfitt, S. A. (eds.) *Boxgrove: A Middle Pleistocene hominid site at Eartham Quarry, Boxgrove, West Sussex*. English Heritage Archaeological Report 17. 197-274.

Pasitschniak-Arts, M. 1993. *Ursus arctos*. *Mammalian Species*. **439**, 1-10.

Pengilly, D. 1984. Development versus functional explanations for patterns of variability and correlation in the dentitions of foxes. *Journal of Mammalogy*. **65(1)**, 34-43.

Persson, I-L., Wikan, S., Swenson, J.E. and Mysterud, I. 2001. The diet of the brown bear *Ursus arctos* in the Pasvik Valley, northeastern Norway. *Wildlife Biology*. **7**, 27-37.

Persson, J., Ericsson, G., and Segerstrom, P. 2009. Human caused mortality in the endangered Scandinavian wolverine population. *Biological conservation*. **142**, 325-331.

Petronio, C., Belluci, L., Martinetto, E., Pandolfi, L. and Salari, L. 2011. Biochronology and palaeoenvironmental changes from the Middle Pliocene to the Late Pleistocene in central Italy. *Geodiversitas*. **33(3)**, 485-517.

Petrucci, M., Cipullo, A., Martinez-Navarro, B., Rook, L. and Sardella, R. 2013. The late Villafranchian (Early Pleistocene) carnivores (Carnivora, Mammalia) from Pirro Nord (Italy). *Palaeontographica, Abt A: Palaeozoology – Stratigraphy*. **298(1-6)**, 113-145.

Pike, A.W.G., Eggins, S., Grün, R., Hedges, R.E.M. and Jacobi, R.M. U-series dating of the Late Pleistocene mammalian fauna from Wood Quarry (Steetley), Nottinghamshire, UK. *Journal of Quaternary Science*. **20(1)**, 59-65.

Post, E., Peterson, R.O., Stenseth, N.C. and McLaren, B.E. 1999. Ecosystem consequences of wolf behavioural response to climate. Nature. 401, 905-907.

Pough, F. H., Janis, C. M. and Heiser, J. B. 2002. *Vertebrate Life*. Prentice Hall. Pp 699.

Preece, R.C. 2001. Molluscan evidence for differentiation of interglacials within the 'Cromerian Complex'. *Quaternary Science Reviews*. **20**, 1643-1656.

Preece, R.C. 2010. The molluscan fauna of the Cromerian type site at West Runton, Norfolk. *Quaternary International.* **228**, 53-62.

Preece, R.C. and Parfitt, S. A. 2000. The Cromer Forest-bed Formation: new thoughts on an old problem. In: Lewis, S. G., Whiteman, C. A. and Preece, R. C. *The Quaternary of Norfolk & Suffolk Field Guide*. Quaternary Research Asociation. Pp 1-29.

Preece, R.C., Parfitt, S.A., Coope, G.R., Penkman, K.E.H., Ponel, P. and Whittaker, J.E. 2009. Biostratigraphic and aminostratigraphic constraints on the age of the Middle Pleistocene glacial succession in north Norfolk, UK. *Journal of Quaternary Science*. **24(6)**, 557-580.

Prestrud, P. and Nilssen, K. 1995. Growth, size and sexual dimorphism in arctic foxes. *Journal of Mammalogy.* **76(2)**, 522-530.

Proctor, C.J. and Smart, P.L. 1996. Uranium series and ESR dating of speleothems from three holes and Tornewton Caves. In: Charman, D.J., Newnham, R.M. and Croot, D.G. (eds.)

The Quaternary of Devon and East Cornwall: field guide. Quaternary Research Association, London, pp 181-186.

Proctor, C. J., Berridge, P. J., Bishop, M. J., Richards, D. A. and Smart, P. L. 2005. Age of Middle Pleistocene fauna and Lower Palaeolithic industries from Kent's Cavern, Devon. *Quaternary Science Reviews*. **24**, 1243-1252.

Pullianen, E. 1975. Wolf ecology in Northern Europe. In: Fox, M.W. (ed.). *The Wild Canids: Their systematic, behavioural ecology and evolution*. Behavioural Science Series. Litton Educational Publishing, Inc. 1975. Pp 292-299.

Raia, P., Piras, P. and Kotsakis, T. 2006. Detection of Plio-Quaternary large mammal communities of Italy. An integration of fossil faunas, biochronology and similarity. *Quaternary Science Reviews*. **25**. 846-854.

Raia, P., Meloro, C. and Barbera, C. 2007. Inconstancy in predator/prey ratios in Quaternary large mammal communities of Italy, with appraisal of mechanics. *Quaternary Research.* **67**, 255-263.

Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *American Naturalist*. **111(981)**, 917-938.

Rathgeber, T. 2008a. Frühe Zeugnisse vom Eichbergschacht (Kat.-Nr 7621/7) bei Undingen (Schwäbische Alb) und Würdigung des biospeläologischen Wirkens von Robert Ernst Wiedersheim. *Beiträge zur Höhlen-und Karstkunde in Südwestdeutschland*. **46**. 5-18.

Rathgeber, T. 2008b. Pleistozäne und Holozäne Tierreste aus Höhlen im Kartenblatt 7521 Reutlingen (Schwäbische Alb). *Laichinger Hohlenfreund.* **43**, 27-34

Razali, N.M. and Wah, Y.B. Power comparisons of Shapiro-Wilk, Kolmogorov-Smirnov, Lilliefors and Anderson-Darling tests. *Journal of Statistical Modeling and Analytics*. **2(1)**, 21-33.

Reinhard, E., de Torres, T. and O'Neil, J. 1996. $^{18}O/^{16}O$ ratios of cave bear tooth enamel: a record of climate variability during the Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **126**, 45-59.

Rensch, B. 1938. Some problems of geographical variation and species formation. *Proceedings of the Linnean Society of London*, 150, 275-285.

Rensch, B. 1960. Evolution above the species level. Columbia University Press, New York. Pp 419.

Reumer, J.F.W., Rook, L., Van der Borg, K., Post, K., Moll, D., De Vos, J., 2003. Late Pleistocene survival of the saber-toothed cat Homotherium in Northwestern Europe. *Journal of Vertebrate Paleontology.* **23(1)**, 260–262.

Reynolds, S.C. 2007. Mammalian body size changes and Plio-Pleistocene environmental shifts: implications for understanding hominin evolution in eastern and southern Africa. *Journal of Human Evolution*, 53, 528-548.

Reynolds, S.H. 1907. A bone cave at Walton, near Clevedon. *Bristol Naturalists' Society*. **4(1)**, 183-187.

Richards, M. P. and Trinkaus, E. 2009. Isotopic evidence for the diets of European Neanderthals and early modern humans. *Proceedings of the National Academy of Sciences.* **106(38)**, 16034-16039.

Ripple, W. J., Larsen, E. J., Renkin, R. A. and Smith, D. W. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation*. **102(3)**, 227-234.

Roberts, M. B. and Parfitt, S. A. 1999. Introduction. In: Roberts, M. B. & Parfitt, S. A. (eds.) *Boxgrove: A Middle Pleistocene hominid site at Eartham Quarry, Boxgrove, West Sussex*. English Heritage Archaeological Report 17. 1-5.

Rodden, M., Rodrigues, F. and Bestelmeyer, S. 2004. Maned wolf *Chrysocyon brachyurus.* In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 38-43.

Rodriguez, J. 2006. Structural and multiple alternative stable states in Middle Pleistocene European mammalian communities. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **239**, 355-373.

Rodríguez, J., Rodríguez-Gómez, G., Martín-González, J. A., Goikoetxea, I., and Mateos, A. 2012. Predator–prey relationships and the role of *Homo* in Early Pleistocene food webs in Southern Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **365-366**, 99-114.

Roe, H. M., Coope, G. R., Devoy, R. J., Harrison, C. J., Penkman, K. E., Preece, R. C. and Schreve, D. C. 2009. Differentiation of MIS 9 and MIS 11 in the continental record:

vegetational, faunal, aminostratigraphic and sea-level evidence from coastal sites in Essex, UK. *Quaternary Science Reviews*. **28(23)**, 2342-2373.

Roemer, G.W., Coonan, T.J., Munson, L. and Wayne, R.K. 2004. Island fox *Urocyon littoralis*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 97-105.

Rogers, L. L. and Mech, L. D. 1981. Interactions of wolves and black bears in northeastern Minnesota. *Journal of Mammalogy*. **62(2)**, 434-436.

Rook, L. 1992. *"Canis" monticinensis* sp. nov., a new Canidae (Carnivora: Mammalia) from the Late Messinian of Italy. *Bolletino della Societa Paleontologia Italiana.* **31**, 151-156.

Rook, L. and Torre, D. 1996a. The Wolf-event in Western Europe and the beginning of the Late Villafranchian. *Neues Jahrb. Geol. Paläontol. Monarshefte.* **8**, 495-501.

Rook, L. and Torre, D. 1996b. The latest Villafranchian – early Galerian small dogs of the Mediterranean area. *Acta Zoologica Cracoviensia*. **39(1)**, 427-434.

Rook, L., Delfino, M., Ferretti, M.P. and Abbazzi, L. 2007. Vertebrate Records – Early Pleistocene. In: Elias, S.A. (ed.) *Encyclopaedia of Quaternary Sciences*. Volume 4. Elsevier, Oxford. Pp 3132-3139.

Rook, L. and Martinez-Navarro, B. 2010. Villafranchian: The long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quaternary International.* **219(1)**, 134-144.

Rook, L., Croitor, R., Delfino, M., Ferretti, M.P., Gallai, G. and Pavia, M. 2013. The Upper Valdarno Plio-Pleistocene vertebrate record: an historical overview, with notes on palaeobiology and stratigraphic significance of some important taxa. *Bollettino della Società Paleontologica Italiana.* **132(1)**, 140-125.

Rose, J. 1985. The Dimlington Stadial/Dimlington Chronozone: a proposal for naming the main glacial episode of the Late Devensian in Britain. *Boreas*. **14(3)**, 225-230.

Rose, J. 2009. Early and Middle Pleistocene landscapes of eastern England. *Proceedings of the Geologist's Association*. **120**, 3-33.

Roseman, C.C. and Weaver, T.D. 2004. Multivariate apportionment of global human craniometric diversity. *American Journal of Physical Anthropology.* **125**. 257-263.

Rosenweig, M.L. 1968. The strategy of body size in mammalian carnivores. *American Midland Naturalist*. **80(2)**, 299-315.

Rowlands, 1971. Radiocarbon evidence of the Age of an Irish Sea Glaciation in the Vale of Clwyd. *Nature*. **230**. 9-11

Rueness, E. K., Jorde, P. E., Hellborg, L., Stenseth, N. C., Ellegren, H., and Jakobsen, K. S. 2003a. Cryptic population structure in a large, mobile mammalian predator: the Scandinavian lynx. *Molecular Ecology*, **12(10)**, 2623-2633.

Rueness, E. K., Stenseth, N. C., O'Donoghue, M., Boutin, S., Ellegren, H., and Jakobsen, K. S. 2003b. Ecological and genetic spatial structuring in the Canadian lynx. *Nature*, **425(6953)**, 69-72.

Rueness, E.K., Gulbrandsen Asmyhr, M., Sillero-Zubiri, C., Macdonald, D.W., Bekele, A., Atickem, A. and Stenseth, N.C. 2011. The cryptic African wolf: Canis aureus lupaster is not a golden jackal and is not endemic to Egypt. *PLOS One.* **6(1)**, 1-5.

Ruff, C.B. 2003. Long bone articular and diaphyseal structure in old world monkeys and apes. II: Estimation of body mass. *American Journal of Physical Anthropology*. **120**, 16-37.

Sablin, M.V. and Klopachev, G.A. 2002. The earliest Ice Age dogs: evidence from Eliseevichi. *Current Anthropology*. **43(5)**, 795-799.

Samuels, J.X., Meachen, J.A. and Sakai, S.A. 2012. Postcranial morphology and the locomotor habits of living and extinct carnivorans. *Journal of Morphology*. **274**, 121-146.

Sand, H., Wikenros, C., Wabakken, P. and Liberg, O. 2006. Effects of hunting group size, snow depth and age on the success of wolves hunting moose. *Animal Behaviour*. **72**, 781-789.

Sardella, R. and Palombo, M.R. 2007. The Pliocene-Pleistocene boundary: which significance for the so called 'Wolf Event'? Evidences from Western Europe. *Quaternaire*. **18(1)**, 65-71.

Savage, R.J.G. 1977. Evolution in carnivorous mammals. *Palaeontology*. **20(2)**, 237-271.

Savolainen, P., Zhang, Y-P., Luo, J., Lundeberg, J. and Leitner, T. 2002. Genetic evidence for an East Asian origin of domestic dogs. *Science.* **298**. 1610-1613.

Schliebe, S., Wiig, Ø., Derocher, A. and Lunn, N. (IUCN SSC Polar Bear Specialist Group) 2008. *Ursus maritimus*. In: IUCN 2013. IUCV Red List of Threatened Species. Version 2013.1. www.iucnredlist.org. Downloaded on 19 August 2013.

Schmidt, P.A. and Mech, L.D. 1997. Wolf pack size and food acquisition. *The American Naturalist.* **150(4)**, 513-517.

Schreve, D. C. 1997. Mammalian biostratigraphy of the later Middle Pleistocene in Britain. Ph.D thesis, University College London, UK.

Schreve, D. C., Currant, A. and Stringer, C. 1999. Conculsion: correlation of the Westbury Cave deposits. In: Andrews, P., Cook, J., Currant, A. P. and Stringer, C. (eds.). *Westbury Cave. The Natural History Museum excavations 1976-1984*. CHERUB. Western Academic & Specialist Press Ltd. 275-285.

Schreve, D.C. 2001a. Differentiation of the British late Middle Pleistocene interglacials: the evidence from mammalian biostratigraphy. *Quaternary Science Reviews*. **20**. 1693-1705

Schreve, D.C. 2001b. Mammalian evidence from the Middle Pleistocene fluvial sequences for complex environmental change at the oxygen isotope substage level. *Quaternary International*. **79**, 65-74.

Schreve, D. C. and Bridgland, D. R. 2002. Correlation of English and German Middle Pleistocene fluvial sequences based on mammalian biostratigraphy. *Geologie en Mijnbouw/ Netherlands Journal of Geosciences*. **81(3-4)**, 357-373.

Schreve, D.C., Bridgland, D.R., Allen, P., Blackford, J.J., Gleed-Owen, C., Griffiths, H.I., Keen, D.H. and White, M.J. 2002. Sedimentology, palaeontology and archaeology of late Middle Pleistocene River Thames terrace deposits at Purfleet, Essex, UK. *Quaternary Science Reviews*. **21**, 1423-1464.

Schreve D.C. 2006. The taphonomy of a Middle Devensian (MIS 3) vertebrate assemblage from Lynford, Norfolk, UK, and its implications for Middle Palaeolithic subsistence strategies. *Journal of Quaternary Science.* **21(5)**, 543-556.

Schreve, D., Howard, A., Currant, A., Brooks, S., Buteux, S., Coope, R., Barnaby, C., Field, M., Greenwood, M., Greig, J. and Toms, P. 2013. A Middle Devensian woolly rhinoceros (*Coelodonta antiquitatis*) from Whitemoor Haye Quarry, Staffordshire (UK): palaeoenvironmental context and significance. *Journal of Quaternary Science.* **28(2)**, 118-130.

Schutt, G. 1973. Revision der Cuon und Xenocyon-Funde (Canidae, Mammalia) aus den altpleistozänen Mosbacher Sanden (Wiesbaden, Hessen). *Mainzer Naturwissenschaftliches Archiv*. **12**, 49-77

Schwarcz , H. P. 1984. Uranium-series dating and stable isotope analyses of calcite deposits. In: Green, H. S. (ed.). *Pontnewydd Cave. A Lower Palaeolithic hominid site in Wales. The first report*. National Museum Wales Qauternary Studies Monograph **1**. 88-97.

Seber, G.A.F. and Lee, A.J. 2003. *Linear regression analysis*. Wiley, U.S.A.

Shackleton, N. J., Berger, A., Peltier, W. R. 1990. An alternative astronomical calibration of the lower Pleistocene timescale based on ODP Site 677. *Transactions of the Royal Society of Edinburgh: Earth Sciences*. **81**, 251-261.

Shapiro, S.S. and Wilk, M.B. 1965. An analysis of variance test for normality. *Biometrika*. **52(3/4)**, 591-611.

Sillero-Zubiri, C. and Gottelli, D. 1994. *Canis simensis. Mammalian Species*. **485**, 1-6.

Sillero-Zubiri, C. 2004. Pale fox *Vulpes pallida*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 199-200.

Sillero-Zubiri, C. and Marino, J. 2004. Ethiopian wolf *Canis simensis*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 167-174.

Skoglund, P., Gotherstrom, A. and Jakobsson, M. 2011. Estimation of population divergence times from non-overlapping genomic sequences: examples from dogs and wolves. *Molecular Biology and Evolution*. **28(4)**, 1505-1517.

Soergel, W. 1928. Ein Kleiner Wolf aus dem Kiesen von Süssenborn. *Zeitschrift der Deutschen Geologische Gesellschaft*. **80**, 227–255.

Smith, D.W., Peterson, R.O., and Houston, D.B. 2003. Yellowstone after wolves. *Bioscience*. **53(4)**, 330-340.

Smith, R.J. 1984. Determination of relative size: the ‘criterion of subtraction’ problem in allometry. *Journal of theoretical Biology.* 108, 131-142.

Smith, R.J. 1993. Logarithmic transformation bias in allometry. *American Journal of Physical Anthropology*. **90**, 215-228.

Smith, R.J. 1994. Regression models for prediction equations. *Journal of Human Evolution*. **26**, 239-244.

Sokal, R.R. and Rohlf, F.J. 1995. *Biometry*. W.H. Freeman and Company. Third edition

Sotnikova, M. 2001. Remains of Canidae from the Lower Pleistocene site of Untermassfeld. In Kahlke, R-D. (Ed.). Das Plestozan von Untermassfled bei Meiningen (Thuringen). Teil 2., Römisch-Germanisches Zentralmuseum, Monographien, 40(2), pp. 607–632.

Sotnikova, M.V., Baigusheva, V.S. and Titov, V.V. 2002. Carnivores of the Khapry Faunal Assemblage and their stratigraphic implications. *Stratigraphy and Geological Correlation.* **10(4),** 375-390.

Sotnikova, M. And Rook, L. 2010. Dispersal of the Canini (Mammalia, Canidae; Caninae) across Eurasia during the Late Miocene to Early Pleistocene. *Quaternary International.* **212(2)**, 86-97.

Sparks, B. W. and West, R. G. 1970. Late Pleistocene deposits at Wretton, Norfolk. I. Ipswichian Deposits. *Phil. Trans. Royal. Soc. Lond. B. Bio. Sci*. **258 (818)**. 1-30.

Spassov, N. and Rook, L. 2006. *Eucyon marinae* sp. nov. (Mammalia, Carnivora), a new canid species from the Pliocene of Mongolia, with a review of forms referable to the genus. *Revisita Italiana di Paleontologia e Stratigraphia.* **112**, 123-133.

Sprugel, D.G. 1983. Correcting for bias in log-transformed allometric equations. *Ecology*. **64(1)**, 209-210.

Spurrell, F. C. J. 1880. On the discovery of the place where Palaeolithic implements were made at Crayford. *Quat. Jou. Geol. Soc*. **36**. 544-549

Stahler, D.R., Smith, D.W. and Guernsey, D.S. 2006. Foraging and feeding ecology of the gray wolf (*Canis lupus*): lessons from Yellowstone National Park, Wyoming, USA. *The Journal of Nutrition*. **136**, 1923S-1926S.

Stains, H.J. 1975. Distribution and taxonomy of the Canidae. In: Fox, M.W.(ed.). *The Wild Canids: Their systematic, behavioural ecology and evolution*. Behavioural Science Series. Litton Educational Publishing, Inc. 1975. Pp 3-26.

Stanley, S.M. 1973. An explanation for Cope's rule. *Evolution*. **27 (1)**, 1-26.

Stiner, M.C., Munro, N., Surovell, T.A., Tchernov, E. and Bar-Yosef, O. 1999. Paleolithic population growth pulses evidenced by small animal exploitation. *Science*. **283**, 190-194.

Stuart, A. J. 1979. Pleistocene occurrences of the European pond tortoise (Emys orbicularis L.) in Britain. *Boreas*. **8(3)**, 359-371.

Stuart, A. J. 1975. The vertebrate fauna of the type Cromerian. *Boreas*. **4(2)**, 63-76.

Stuart, A. J. 1976. The history of the mammal fauna during the Ipswichian/Last Interglacial in England. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*. **276(945)**, 221-250.

Stuart, A. J. 1981. A comparison of the Middle Pleistocene mammal faunas of Voigtstedt (Thuringia, GDR) and West Runton (Norfolk, England).*Quartärpaläontologie*. **4**, 155-163.

Sutcliffe, A. J., Currant, A. P. and Stringer, C. B. 1987. Evidence of sea-level change from coastal caves with raised beach deposits, terrestrial faunas and dated stalagmites. *Progress in Oceanography*. **18**. 243-271.

Stuart, A. J. 1995. Insularity and Quaternary vertebrate faunas in Britain and Ireland. *Geological Society, London, Special Publications.* **96(1)**, 111-125.

Stuart, A. J. and Lister, A. M. 2010. The West Runton Freshwater Bed and the West Runton Mammoth: summary and conclusions. *Quaternary International*. **228**. 241-248.

Stuart, A. J., and Lister, A. M. 2011. Extinction chronology of the cave lion *Panthera spelaea*. *Quaternary Science Reviews*, **30(17)**, 2329-2340.

Stuart, C. and Stuart, T. 2004. Cape fox *Vulpes chama*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 189-193.

Swenson, J. E., Sandegren, F., Bjärvall, A., Söderberg, A., Wabakken, P., and Franzén, R. 1994. Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. *Biological Conservation*, **70(1)**, 9-17.

Swenson, J.E., Sandegren, F., Bjarvall, A., Franzen, R., Soderberg, A. and Wabakken, P. 1999. Status and management of the brown bear in Sweden. In: Servheen, C., Herrero, S. and Peyton, B. *Bears: status survey and action plan*. IUCN. Pp 111-113.

Tabachnick, B.G. and Fidell, L.S. 1996. *Using multivariate statistics*. Harper Collins, U.S.A. Third edition.

Tedford, R. H. and Qui, Z. 1996. A new canid genus from the Pliocene of Yushe, Shanxi Province. *Vertebrata PalAsiatica*. **34**, 27-40.

Tedford, R. H. and Martin, J. 2001. Plionarctos, a tremarctine bear (Ursidae: Carnivora) from western North America. *Journal of Vertebrate Paleontology*. **21(2)**, 311-321.

Tedford, R. H., Wang, X. And Taylor, B. E. 2009. Phylogenetic systematic of the North American fossil Caninae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History.* **325**. 218 pp.

Thenius, E. 1954. Die Caniden (mammalia) aus dem Altquartär von Hundsheim (Niederösterreich) nebst Bemerkungen sur Stammesgeschichte der Gattung Cuon. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 99, 230-286.

Thouveny, N. and Bonifay, E. 1984. New chronological data on European Plio-Pleistocene faunas and hominid occupation sites. *Nature*. **308**, 355-358.

Torre, D. 1967. I Cani Villafranchiani della Toscana. Palaeontogr Ital. **63**, 113–138

Torre, D. 1979. The Ruscinian and the Villafranchian dogs of Europe. *Bolletino della Societa Paleontologia Italiana*. **18(2)**, 162-165.

Treves, A., Jurewicz, R. R., Naughton-Treves, L., Rose, R. A., Willging, R. C., and Wydeven, A. P. 2002. Wolf depredation on domestic animals in Wisconsin, 1976-2000. *Wildlife Society Bulletin*, 30 (1), 231-241.

Treves, A. and Karanth, K.U. 2003. Human-Carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*. **17 (6)**, 1491-1499.

Trouwborst, A. 2010. Managing the carnivore comeback: international and EU species protection law and the return of lynx, wolf and bear to western Europe. *Journal of environmental law*. **22(3)**, 347-372.

Turner, A. 1981. Aspects of the Palaeoecology of large predators, including Man, during the British Upper Pleistocene, with particular emphasis on predator-prey relationships. Ph.D. thesis, University of Sheffield, UK.

Turner, A. 1984. Dental sex dimorphism in European lions (*Panthera leo* L.) of the Upper Pleistocene: palaeoecological and palaeoethological implications. *Annales Zoologici Fennici*. **21**. 1-8.

Turner, A. 1995a. Evidence for Pleistocene contact between the British Isles and the European continent based on distributions of larger carnivores. Geological Society, London, Special Publications. 96, 141-149.

Turner, A. 1995b. The Villafranchian large carnivore guild: geographic distribution and structural evolution. *Il Quaternario*. **8(2)**, 349-356.

Turner, A. 1999. Larger carnivores (Mammalia, Carnivora) from Westbury cave. In Andrews, P., Cook, J., Currant, A. P. and Stringer, C. (eds.). *Westbury Cave. The Natural History Museum excavations 1976-1984*. CHERUB. Western Academic & Specialist Press Ltd. 175-193.

Turner, A. and Antón, M. 1996. The giant hyaena *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). *Geobios*, **29(4)**, 455-468.

Turner, A. and Antón, M. 1997. The big cats and their fossil relatives. Columbia University Press, New York.

Turner, A. 2009. The evolution of the guild of large Carnivora of the British Isles during the Middle and Late Pleistocene. *Journal of Quaternary Science*, **24(8)**, 991-1005.

Turner, C. 1998. Volcanic maars, long Quaternary sequences and the work of the INQUA subcommission on European Quaternary stratigraphy. *Quaternary International.* **47/48**, 41-49.

U.S. Fish and Wildlife Service, 1987. Northern Rocky Mountain Wolf Recovery Plan. U.S. Fish and Wildlife Service, Demver, Colorado. Pp 119.

Van Valkenburgh, B. 1985. Locomotor diversity within past and present guilds of large predatory mammals. *Paleobiology*. **11(4)**, 406-428.

Van Valkenburgh, B. 1987. Skeletal indicators of locomotor behaviour in living and extinct carnivores. *Journal of Vertebrate Paleontology*. **7(2)**, 162-182.

Van Valkenburgh, B. 1988a. Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology*. **14(2)**, 155-173.

Van Valkenburgh, B. 1988b. Incidence of tooth breakage among large, predatory mammals. The American Naturalist. 131(2), 291-302.

Van Valkenburgh, B. 1989. Carnivore dental adaptations and diet: a study of trophic diversity within guilds. In: Gittleman, J.L. (ed.) *Carnivore behaviour, ecology and evolution*. Part III. Spinger US. pp 410-436.

Van Valkenburgh, B. 1990. Skeletal and dental predictors of body mass in carnivores. In: Damuth, J. and MacFadden, B.J. (eds.) *Body size in mammalian paleobiology: estimation and biological implications.* Cambridge University Press. Pp 181-205.

Van Valkenburgh, B. 1991. Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): Evolutionary interactions among sympatric predators. *Paleobiology*. **17(4)**, 340-362.

Van Valkenburgh, B. and Hertel, F. 1993. Tough times at La Brea: tooth breakage in large carnivores of the Late Pleistocene. *Science*. **261(5120)**, 456-459.

Van Valkenburgh, B. and Koepfli, K-P. 1993. Cranial and dental adaptations to predation in canids. In: Dunstone, N., Gorman, M. L. (Eds.). *Mammals as predators*. Symposium of the Zoological Society, London. **65**, pp. 15-37.

Van Valkenburgh, B. and Wayne, R.K. 1994. Shape divergence associated with size convergence in sympatric East African jackals. *Ecology*. **75(6)**, 1567-1581.

Van Valkenburgh, B. 1996. Feeding behaviour in free-ranging, large African carnivores. *Journal of Mammalogy*. **77(1)**, 240-254.

Van Valkenburgh, B. and Sacco, T. 2002. Sexual dimorphism, social behaviour, and intrasexual competition in large Pleistocene carnivorans. *Journal of Vertebrate Paleontology*, 22 (1), 164-169.

Van Valkenburgh, B., Wang, X. And Damuth, J. 2004. Cope's rule, hypercarnivory, and extinction in North American canids. *Science*. **306**, 101-104.

Vigne, J-D. 2005. The Magdalenian dog humerus of Erralla (Gipuzkoa, Spain) and the Late Glacial wolf domestication in Europe. *Munibe (Antropologia-Arkeologia)*. **57**, 279-287.

Vila, C. 1997. Multiple and ancient origins of the domestic dog. *Science*. **276**, 1687-1689.

Voigt, D. R., Kolenosky, G. B., Pimlott, D. H. 1976. Changes in summer foods of wolves in central Ontario. *Journal of Wildlife Management*. **40(4)**, 663-668.

Von den Driesch, A. 1976. *A guide to the measurement of animal bones from archaeological sites*. Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, U.S.A.

Vos, J. 2000. Food habits and livestock depredation of two Iberian wolf packs (*Canis lupus signatus*) in the north of Portugal. *Journal of Zoology*. **251**, 457-462.

Wabakken, P., Sand, H., Liberg, O. and Bjärvall. 2001. The recovery, distribution, and population dynamics of wolves in the Scandinavian peninsula, 1978-1998. *Canadian Journal of Zoology*. **79**, 710-725.

Wagner, G.A., Maul, L.C., Löscher, M. and Schreiber, H.D. 2011. Mauer – the type site of Homo Heidelbergensis: palaeoenvironments and age. *Quaternary Science Reviews*. **30**, 1464-1473.

Walsberg, G.E. 1983. Coat colour and solar heat gain in animals. *BioScience*. **33(2)**, 88-91.

Walton, L.R., and Joly, D.O. 2003. *Canis mesomelas. Mammalian Species*. **715**, 1-9.

Wang, X. and Tedford, R.H. 2007. In: Jensen, P. (ed.) *The Behavioural Biology of Dogs*. CAB International. Pp 3-20.

Ward, O.G. and Wurster-Hill, D.H. 1990. *Nyctereutes procyonoides. Mammalian Species*. **358**, 1-5.

Wenzel, S. 1998. Die mittelpalaolithischen Funde aus dem jungpleistozanen Travertin von Stuttgart-Unterturkeim. *Jh. Gesellschaft für Naturkunde. Württemberg*. **154**, 171-190.

Werdelin, L. 1989. Constraint and adaptation in the bone-cracking canid Osteoborus (Mammalia: Canidae). *Paleobiology*. **15(4)**, 1387-401.

Werdelin, L. and Lewis, M. E. 2005. Plio-Pleistocene Carnivora of eastern Africa: species richness and turnover patterns. *Zoological Journal of the Linnean Society*. **144(2)**, 121-144.

West, R. G. 1980. *Pleistocene geology and biology*. Longman. Pp 379.

Whidbey, J. 1823. On some fossil bones discovered in cavern in the lime-stone quarries of Oreston. *Philosophical Transactions of the Royal Society, London*. **113**, 78-90.

White, C.R. and Seymour, R.S. 2003. Mammalian basal metabolic rate is proportional to body mass2/3. *PNAS*. **100(7)**, 4046-4049.

White, M.J. and Schreve, D.C. 2000. Island Britain-peninsula Britain: palaeogeography, colonisation and Lower Palaeolithic settlement of the British Isles. *Proceedings of the Prehistoric Society*. **66**, 1-28.

White, M. and Petitt, P. 2012a. The British Palaeolithic, human socieities at the edge of the Pleistocene world. Routledge, Oxon, U.K. Pp 592.

White, M. and Petitt, P. 2012b. Ancient digs and modern myths: the age and context of the Kent's Cavern 4 maxilla and the earliest Homo sapiens specimens in Europe. *European Journal of Archaeology*. **15**, 1-30.

Wilson, E. and Reynolds, S. H. 1902. Uphill bone-caves. *Proceedings of the Bristol Naturalists' Society.* **9(3)**, 152-160.

Woodroffe, R., McNutt, J.W. and Mills, M.G.L. 2004. African wild dog *Lycaon pictus*. In: Sillero-Zubiri, C., Hoffmann, M. and Macdonald, D.W. (eds.) *Canids: Foxes, Wolves, Jackals and Dogs. Status survey and conservation action plan*. IUCN publications, Cambridge, U.K. Pp 174-183.

Zagwijn, W.H. 1989. Vegetation and climate during warmer intervals in the Late Pleistocene of western and central Europe. *Quaternary International.* **3/4**, 57-67.

Zar, J.H. 2010. Biostatistical Analysis. Fifth edition. Pearson Prentice Hall, U.S.A.

Ziegler, R. 1996. Die Großsäuger aus der Frühwürm-zeitlichen Fauna von der Villa Seckendorff in Stuttgart-Bad Canstatt. *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontolgie)*. **237**, 1-67

Zorzin, R., Santi, G. and Rossi, M. 2003. I principali mammiferi quaternari della Grotta del Cerè (Monti LessiniVR) conservati presso il Museo Civico di Storia Naturale di Verona. *Thalassia Salentina*. **26**, 183-190.

Appendix I. Species lists for sites included in the analysis

British sites

1. West Runton, Norfolk. Mammalian fauna from West Runton (Stuart and Lister, 2010).

Canis mosbachensis	*Nyctalus noctula*
Lutra simplicidens	*Sorex runtonensis*
Pannonictis pliocaenica	*Sorex savini*
Martes martes	*Sorex* cf. *minutus*
Mustela nivalis	*Macroneomys brachygnathus*
Mustela erminea	*Neomys newtoni*
Ursus sp.	*Desmana* sp.
Crocuta crocuta	*Talpa minor*
Cf. *Pachycrocuta brevirostris*	*Talpa europaea*
Felis sp.	*Erinaceus* sp.
Felis cf. *lunensis*	*Macaca sylvanus*
Cf. *Lynx sp.*	*Lepus* sp.
Panthera leo	*Sciurus whitei*
Panthera gombaszoegensis	*Castor fiber*
Homotherium latidens	*Trogontherium cuvieri*
Mammuthus trogontherii	*Cricetus runtonensis*
Equus cf. *süssenbornensis*	*Cricetulus migratorius*
Equus cf. *altidens*	*Pliomys episcolpalis*
Stephanorhinus hundsheimensis	*Clethrionomys hintonianus*
Stephanorhinus sp. aff. *S. etruscus/hundsheimensis*	*Mimomys savini*
Sus scrofa	*Microtus 'arvalinus'*
Dama sp.	*Microtus gregaloides*
Praemegaceros verticornis	*Microtus arvalidens*
Megaloceros savini	*Microtus ratticepoides*
Cervalces latifrons	*Apodemus sylvaticus*
Cervus elaphus	
Capreolus capreolus	
Bison cf. *schoetensacki*	

2. Westbury-sub-Mendip, Somerset. Mammalian fauna from the Calcareous Member at Westbury-sub-Mendip (Andrews *et al*., 1999). Numbers shown are related to the NHM excavation Units. 'Bed' indicates Bishop (1982) stratigraphy.

Calcareous Member	**Calcareous Member Cont.**
Canis lupus mosbachensis Unit 2, 12, 13, 14, 18, 19/14, 19/15, 19 (W1A), 19, Bed 4a	*Ochotona* cf. *pusilla* 14, 15/1, 15/8
Xenocyon lycaonoides Unit 18, 19, Bed 4b	*Lepus timidus* 11/4, 11/1, 12, 13, 14, 15/1, 15/8
Homotherium latidens Unit 18, 19/8, 19/14, Bed 4a	*Cricetulus migratorius* 13, 14, 15/1
Panthera gombaszoegensis Unit 11, 18/6, 18, 19/5, 19/14, 19, Beds 4a, 4b.	*Lemmus/Myopus* sp. 14, 15/8
Panthera leo Unit 19/6, 19/8, 19/14, 19, Bed 4a	*Dicrostonyx torquatus* 13, 15/8
Felidae sp. Unit 2, 13, 18, 19/14, 19	*Clethrionomys glareolus* 11/4, 11/1, 12,

	13, 15/1, 15/8
Crocuta crocuta Bed 4b	*Pliomys episcopalis* 11/4, 11/1, 15/1, 15/8
Ursus deningeri all units Calc. Memb	*Arvicola terrestris cantiana* 11/4, 11/1, 12, 13, 15/1, 15/2, 15/5, 15/8
Mustela erminea 11/4, 12, 13, 14, 15/1, 15/2, 15/5, 15/8	*Microtus subterraneus* 11/1, 12, 14, 15/1, 15/2, 15/5, 15/8
Mustela nivalis 11/4, 11/1, 12, 14, 15/1, 15/2, 15/5, 15/8	*Microtus gregalis* 11/1, 12, 13, 14, 15/1, 15/8
Martes martes 11/4, 15/1	*Microtus* cf. *agrestris* 11/4,
Cervus e*laphus* 11	*Microtus oeconomus* 11/4, 11/1, 12, 13, 15/1, 15/8
Dama dama 11	*Microtus* sp (*arvalinus*) 11/4, 11/1, 12, 13, 15/1, 15/2, 15/5, 15/8
Capreolus capreolus 19	*Apodemus sylvaticus* 11/4, 11/1, 12, 13, 15/1, 15/2, 15/5
Bos (Bison) schoetensacki 11, 15/2, 15/4	*Muscardinus avellanarius* 11/1, 12, 15/1
Cf *Soergelia elizabethae* 19	*Eliomys quercinus* 15/1
Ovis or *Capra* 14, 19	*Scirius vulgaris* 13, 14, 15/2, 15/5
Erinaceus europaeus 12, 14, 15/2, 15/5, 15/8	*Myotis bechsteinii* 11/4
Talpa sp. 11/4, 11/1, 12, 13, 14, 15/1, 15/2, 15/8	*Myotis emarginatus* 11/4
Desmana moschata 13, 14, 15/8	*Myotis nattereri* 11/4
Neomys sp. 11/4, 13, 15/8	*Eptesticus serotinus* 11/4
Sorex minutus 11/4, 11/1, 13, 14, 15/1, 15/2, 15/5, 15/8	*Barbastella barbastellus* 11/4
Sorex runtonensis 11/4, 12, 13, 14, 15/1, 15/2, 15/5, 15/8	*Plecotus auritus* 11/4
Sorex sp. 11/4, 11/1	
Depranosorex savini 11/4, 11/1, 12, 13, 14, 15/1, 15/2, 15/5, 15/8	

3. Boxgrove (Amey's Eartham Pit), West Sussex. Fauna from canid-bearing units 4b, 4c, 5a, 5b (GTP 17) and 6 at Boxgrove (Roberts and Parfitt, 1999).

Canis mosbachensis	*Arvicola terrestris cantiana*
Ursus deningeri	*Microtus (Terricola)* cf *M. (t.) subterraneus*
Mustela erminea	*Microtus agrestis*
Mustela lutreola	*Microtus arvalis*
Mustela nivalis	*Microtus gregalis (gregaloides morphotype)*
Mustela sp.	*Microtus oeconomus*
Meles meles	*Castor fiber*
Crocuta crocuta	*Muscardinus avellanarius*
Felis cf sylvestris	*Eliomys quercinus*
Cf *Panthera leo*	*Sicista* cf *betulina*
Carnivora*,* gen. et. sp. indet.	*Apodemus maastrichtiensis*
Elephantid sp*.*	*Apodemus sylvaticus*
Elephantidae gen. et. sp. indet.	*Lepus timidus*
Equus ferus	*Erinaceus sp.*
Stephanorhinus hundsheimensis	*Oryctolagus* cf *O. cuniculus*
Cervus elaphus	*Neomys sp.*

Dama dama	*Sorex minutus*
Capreolus capreolus	*Sorex runtonensis*
Megaloceros cf verticornis	*Sorex (Drepanosorex)* sp.
Cervidae, gen. et. sp. indet.	*Talpa europaea*
Bison sp.	*Talpa minor*
Caprinae gen. et. sp. indet.	*Plecotus auritus*
Sciurus sp.	*Myotis mystacinus*
Myopus schisticolor	*Myotis bechsteini*
Lemmus lemmus	
Lemmus or Myopus spp.	
Clethrionomys glareolus	
Clethrionomys rufocanus	
Pliomys episcolpalis	

4. Sidestrand, Norfolk. Mammalian fauna present in the Sidestrand Hall Member (Preece and Parfitt, 2000; Preece *et al*., 2009).

Canis mosbachensis	*Clethrionomys glareolus*
Felis sylvestris	*Arvicola terrestris cantiana*
Ursus deningeri	*Microtus gregaloides*
Equus süssenbornensis	*Microtus oeconomus*
Stephanorhinus cf. *hundsheimensis*	*Microtus* sp.
Megaloceros sp.	*Apodemus sylvaticus*
Bison priscus	
Sorex cf. *runtonensis*	

5. Cudmore Grove, Essex. Mammalian fauna present at Cudmore Grove (Roe *et al.,* 2009).

Canis mosbachensis	*Sciurus vulgaris*
Ursus arctos	*Castor fiber*
Meles meles	*Clethrionomys glareolus*
Mustela cf *putorius*	*Arvicola terrestris cantiana*
Equus ferus	*Microtus agrestis*
Capreolus capreolus	Microtus agrestis or M. arvalis
Sorex cf *araneus*	*Microtus* sp.
Sorex cf *minutus*	*Apodemus* cf *sylvaticus*
Neomys cf *browni*	*Macaca sylvanus*
Crocidura cf *leucodon*	
Eptesicus cf *serotinus*	

6. Grays Thurrock, Essex. Mammalian fauna from Grays Thurrock (Schreve, 1997).

Canis mosbachensis	*Capreolus capreolus*
Vulpes vulpes	Cervidae sp
Ursus arctos	*Bos primigenius*
Lutrinae sp.	Bovidae sp.
Crocuta crocuta	*Sorex* sp. indet
Palaeoloxodon antiquus	*Neomys* cf. *browni*
Elephantidae sp.	*Crocidura* sp. indet.
Equus ferus	*Macaca sylvanus*

Stephanorhinus hemitoechus	*Homo* sp
Stephanorhinus kirchbergensis	*Castor fiber*
Stephanorhinus sp.	*Clethrionomys* cf *glareolus*
Sus scrofa	*Arvicola terrestris cantiana*
Megaloceros giganteus	*Microtus agrestis*
Dama dama	Microtus sp.
Cervus elaphus	*Apodemus* cf *sylvaticus*
Alces cf *alces*	*Tursiops truncatus*

7. Pontnewydd Cave, Denbighshire. Mammalian fauna of preservation types I (Intermediate complex) and II (Lower Breccia) (Currant, 1984). Preservation types I and II are now considered to be close in age and are combined into one preservation type (Campbell and Bowen, 1989)

Preservation type I: Intermediate Complex:	**Preservation type II: Lower Breccia:**
Canis lupus	*Canis lupus*
Ursus sp.	*Ursus* sp
Panthera aff. pardus	Cf *Crocuta crocuta*
Homo neanderthalensis	*Panthera* aff. *pardus*
Equus sp.	*Equus* sp.
Stephanorhinus hemitoechus	*Stephanorhinus hemitoechus*
Capreolus capreolus	*Stephanorhinus* cf. *kirchbergensis*
Castor fiber	*Cervus elaphus*
Arvicola cantiana	*Bovini* (*Bos* or *Bison* sp.)
Microtus gregalis	*Lemmus lemmus*
Apodemus cf. *sylvaticus*	*Arvicola* sp.
	Microtus gregalis
	Microtus oeconomus
	Ochotona sp.

8. Bleadon Cave, Somerset. Mammalian fauna from Bleadon Cavern (Currant, 2004).

Lepus timidus	*Panthera pardus*
Citellus cf *citellus*	*Palaeoloxodon antiquus*
Microtus oeconomus	*Mammuthus trogontherii* (was *primigenius*)
Canis lupus	*Equus ferus*
Vulpes vulpes	Rhinocerotidae sp. indet.
Ursus arctos	*Sus scrofa*
Mustela putorius	*Cervus elaphus*
Crocuta crocuta	*Capreolus capreolus*
Felis sylvestris	*Bos primigenius*
Panthera leo	*Bison* cf *priscus*

9. Hutton Cave, Somerset. Mammalian fauna of Hutton Cave (Currant, 2004).

Canis lupus	*Equus ferus*
Vulpes vulpes	*Sus scrofa*
Crocuta crocuta	*Cervus elaphus*
Panthera leo	*Lepus* sp.
Felis sylvestris	*Allocricetus bursae*

Mammuthus trogontherii (was *primigenius*)	*Dicrostonyx torquatus*

10. Tornewton Cave, Otter Stratum (Vivian's Vault), Devon. Mammalian fauna from Tornewton Cave Otter stratum (Schreve, 1997).

Canis lupus	*Sorex araneus*
Vulpes vulpes	*Crocidura russula*
Meles meles	*Crocidura* sp.
Cyrnaonyx antiqua	*Apodemus sylvaticus*
Erinaceous europaeus	

11. Iford (Uphall Pit), Essex. Mammalin fauna from Uphall Pit, Ilford (Schreve, 1997).

Canis lupus	*Megoloceros giganteus*
Ursus arctos	*Cervus elaphus*
Panthera leo	*Capreolus capreolus*
Palaeoloxodon antiquus	*Bos primigenius*
Mammuthus trogontherii (was *primigenius*)	*Bison priscus*
Elephantidae sp.	Bovidae sp.
Equus ferus	*Castor fiber*
Stephanorhinus hemitoechus	*Arvicola terrestris cantiana*
Stephanorhinus kirchbergensis	
Coelodonta antiquitatis	
Stephanorhinus *sp.*	

12. Marsworth, Buckinghamshire. Mammalian fauna present in the Lower channel, Marsworth (Murton *et al*., 2001).

Canis lupus	*Bos primigenius*
Vulpes vulpes	Cf *Bison priscus*
Ursus arctos	Bovidae sp.
Panthera leo	Leporidae sp.
Palaeoloxodon antiquus	*Neomys fodiens*
Mammuthus trogontherii	*Arvicola terrestris cantiana*
Equus ferus	*Microtus oeconomus*
Cervus cf. *elaphus*	Microtus sp.
Cervidae sp. Indet	

13. Crayford Brickearths, Kent. Mammalian fauna of Crayford (Kennard, 1944; Schreve, 1997).

Canis lupus	*Cervus elaphus*
Canis sp.	*Bos primigenius*
Ursus arctos	*Bison priscus*
Crocuta crocuta	Bovidae sp. indet.
Panthera leo	*Ovibos moschatus*
Palaeoloxodon antiquus	*Sorex* cf. *araneus*
Mammuthus trogontherii (was *primigenius*)	*Microtus oeconomus*
Elephantidae sp. indet.	*Microtus* sp. indet.
Coelodonta antiquitatis	*Citellus citellus*

Rhinocerotidae sp.	*Dicrostonyx* cf. *torquatus*
Equus ferus	*Lemmus lemmus*
Stephanorhinus hemitoechus	*Homo* sp. (artefacts)
Stephanorhinus kirchbergensis	
Coelodonta antiquitatis	
Rhinocerotidae sp. indet.	
Megaloceros giganteus	

14. Clevedon Cave, Somerset. Mammalian fauna from Clevedon Cave (Reynolds, 1907).

Canis lupus	*Microtus oeconomus*
Vulpes vulpes	*Lepus cuniculus* (= cf. *O. cuniculus*, modern?)
Alopex lagopus	
Ursus arctos	
Equus ferus	
Microtus agrestis	

15. Barrington Beds, Cambridgeshire. Mammalian fauna from the Barrington Beds (Gibbard and Stuart 1975; Boylan 1981).

Canis lupus	*Cervus elaphus*
Vulpes vulpes	*Bos primigenius*
Ursus arctos	*Bison priscus*
Meles meles	*Arvicola terrestris cantiana*
Crocuta crocuta	*Microtus agrestis*
Panthera leo	
Palaeoloxodon antiquus	
Stephanorhinus hemitoechus	
Hippopotamus amphibius	
Megaloceros giganteus	

16. Joint Mitnor Cave, Devon. Mammalian fauna from Joint Mitnor Cave (Currant and Jacobi, 2001).

Canis lupus	*Cervus elaphus*
Vulpes vulpes	*Dama dama*
Ursus arctos	*Megaloceros giganteus*
Meles meles	*Bison priscus*
Crocuta crocuta	*Sorex araneus*
Felis sylvestris	*Lepus timidus*
Panthera leo	*Clethrionomys glareolus*
Palaeoloxodon antiquus	*Arvicola terrestris cantiana*
Stephanorhinus hemitoechus	*Microtus agrestis*
Sus scrofa	*Apodemus sylvaticus*
Hippopotamus amphibius	

17. Bacon Hole, Gower. Mammalian fauna from the canid-bearing units of the Grey Clays, Silts and Sands (unit G), Upper Sands (unit H) and Upper Cave Earth (unit I) (Currant and Jacobi, 2001).

Fauna from unit G	**Fauna from units H & I**
Sorex araneus	*Arvicola terrestris cantiana*
Clethrionomys glareolus	*Microtus oeconomus*
Arvicola terrestris cantiana	*Canis lupus*
Microtus oeconomus	*Crocuta crocuta*
Microtus agrestis	*Palaeoloxodon antiquus*
Apodemus sylvaticus	*Stephanorhinus hemitoechus*
Palaeoloxodon antiquus	*Cervas elaphus*
Mammuthus primigenius	*Bison priscus*
Stephanorhinus hemitoechus	
Crocuta crocuta	
Canis lupus	
Meles meles	
Cervus elaphus	
Capreolus capreolus	
Bison priscus	

18. Minchin Hole, Gower. Mammalian fauna from the canid-bearing units 7 and 8, Minchin Hole (Sutcliffe *et al*., 1987).

Neritoides Beach (Unit 7) :	**Earthy Breccia Series (Unit 8):**
Crocuta crocuta	*Canis lupus*
Panthera leo	*Vulpes vulpes*
Dama dama	*Crocuta crocuta*
Sus scrofa	*Panthera leo*
Apodemus sylvaticus	*Stephanorhinus hemitoechus*
Clethrionomys glareolus	*Palaeoloxodon antiquus*
Microtus agrestis	Cervidae
	Clethrionomys glareolus
	Microtus agrestis
	Microtus oeconomus

19. Banwell Bone Cave, Somerset. Mammalian fauna Banwell Bone Cave (Currant and Jacobi, 2001).

Canis lupus	*Lepus timidus*
Vulpes vulpes	*Microtus oeconomus*
Gulo gulo	
Ursus arctos	
Rangifer tarandus	
Bison priscus	

20. Bosco's Den, Gower. Mammalian fauna from the canid-bearing beds of 3 and 8 (Campbell and Bowen, 1989).

Bed 3	**Bed 8:**
Canis lupus	*Canis lupus*
Vulpes vulpes	*Bos* sp.
Ursus sp.	*Rangifer tarandus*
Bos sp	
Cervus sp	
Arvicola sp	

21. Steetley Quarry Cave, Nottinghamshire. Mammalian fauna from Steetley Quarry (Pike *et al.,* 2005).

Canis lupus	*Bison* sp.
Vulpes vulpes	
Ursus arctos	
Rangifer tarandus	

22. Stump Cross Cave, North Yorkshire. Mammalian fauna from the Bowling Alley Passage, Stump Cross Cave (Gilmour *et al*., 2007).

Canis lupus	Cf *Bison priscus*
Vulpes vulpes	
Gulo gulo	
Rangifer tarandus	

23. Windy Knoll, Derbyshire. Mammalian fauna at Windy Knoll (Dawkins, 1875, 1877).

Canis lupus	*Arvicola terrestris cantiana*
Vulpes vulpes	*Lepus timidus*
Ursus arctos	
Rangifer tarandus	
Bison priscus	

24. Wretton, Norfolk. Mammalian fauna from Wretton (Stuart, 1977).

Canis lupus	*Rangifer tarandus*
Alopex lagopus	*Bison priscus*
Mammuthus primigenius	
Equus callabus	

25. Black Rock Quarry, Pembrokeshire. Mammalian fauna from Black Rock Quarry (Dawkins, 1874).

Canis lupus	*Coelodonta antiquitatis*
Crocuta crocuta	*Rangifer tarandus*
Ursus sp.	
Mammuthus primigenius	

26. Kents Cavern, Devon. Mammalian fauna from the Cave Earth at Kents Cavern (Keen, 1998).

Canis lupus	*Equus ferus*
Crocuta crocuta	*Megaloceros giganteus*
Ursus arctos	*Homo* sp.
Coelodonta antiquitatis	
Mammuthus primigenius	

27. Oreston Cave, Devon. Generalised fauna from Oreston Cave (Clift, 1823; Boylan, 1981). Letter denotes cavern where species found based on Clift (1823).

Canis lupus E	*Equus ferus*
Vulpes vulpes E	*Bison sp.*
Crocuta crocuta B, E	Cervidae
Panthera leo	*Arvicola sp.*
Ursus arctos (U. priscus and U. spelaeus)	
Stephanorhinus hemitoechus	

28. Paviland, Gower. Mammalian fauna present at Paviland (Jacobi and Higham, 2008).

Canis lupus	*Homo* sp.
Ursus arctos	
Crocuta crocuta	
Coelodonta antiquitatis	
Rangifer tarandus	

29. Pin Hole Cave, Derbyshire. Mammalian fauna from the Lower Cave Earth at Pin Hole Cave (Jacobi *et al*., 1998; Currant and Jacobi, 2001).

Canis lupus	*Bison priscus*
Vulpes vulpes	*Megaloceros giganteus*
Ursus arctos	*Rangifer tarandus*
Crocuta crocuta	*Lepus timidus*
Panthera leo	*Spermophilus major*
Mustela erminea	*Homo* sp (artefacts)
Mustela putorius	
Mammuthus primigenius	
Coelodonta antiquitatis	
Equus ferus	

30. Sandford Hill, Somerset. Mammalian fauna of Sandford Hill (Currant, 2004).

Canis lupus	*Coelodonta antiquitatis*
Vulpes vulpes	*Rangifer tarandus*
Panthera leo	*Cervus elaphus*
Crocuta crocuta	*Bison priscus*
Ursus arctos	*Lepus timidus*
Equus ferus	

31. Uphill Quarry, Somerset. Table 5.41. Mammalian fauna of Uphill Quarry cave 7/8 (Harrison, 1977). *modern contaminant.

Canis lupus	*Equus* sp
Vulpes vulpes	*Bison priscus*
Ursus sp.	*Cervus* (? *elaphus*)
Panthera leo	*Rangifer tarandus*
Crocuta crocuta	*? Megaloceros giganteus*
*Meles meles**	*Lemmus lemmus*
Mammuthus primigenius	
Coelodonta antiquitatis	

32. Cae Gwyn Cave, Clwyd. Mammalian fauna of Cae Gwyn Cave (Rowlands, 1971; Capmbell & Bowen, 1989). *Modern contaminant

Canis lupus	*Equus caballus*
Vulpes vulpes	*Bos* sp
Ursus sp	*Megaloceros giganteus*
Crocuta crocuta	*Cervus elaphus*
Panthera leo	*Capreolus capreolus**
Felis sylvestris	*Rangifer tarandus*
Meles sp.*	*Sus scrofa**
Coelodonta antiquitatis	
Mammuthus primigenius	

33. Ogof yr Ychen, Caldey Island, Pembrokeshire. Mammalian fauna from Ogof-yr-Ychen, all chambers (Bateman, 1973). * Modern contaminant

Canis lupus	*Coelodonta antiquitatis*
Vulpes vulpes	*Bison priscus*
Ursus spelaeus	*Bos primigenius*
Ursus arctos	*Cervus elephas*
Gulo gulo	*Capreolus capreolus**
Panthera leo	*Sus scrofa**
Felis sylvestris	*Erinaceus europaeus**
Crocuta crocuta	*Talpa europaea**
*Meles meles**	*Microtus arvallis*

34. Sun Hole, Somerset. Mammalian fauna from unit 1 at Sun Hole (Collcutt *et al.,* 1981).

Canis lupus	*Apodemus sylvaticus*
Vulpes vulpes	*Dicrostonyx torquatus*
Ursus arctos	*Lemmus lemmus*
Mustela nivalis	*Clethrionomys glareolus*
Felis sylvestris	*Arvicola terrestris*
Homo sapiens	*Microtus* sp. either *M. arvalis* or *M. gregalis*
Equus ferus	*Microtus gregalis*
Rangifer tarrandus	*Microtus oeconomus*
Saiga tatarica (layer 5, unit 1)	*Ochotona pusilla*
Castor fiber	*Lepus timidus*

Talpa europaea

Mainland European sites

35. Val di Magra, Tuscany, Italy (Olivola Faunal Unit). Mammalian fauna from Val di Magra, Olivola F.U. (Forsyth Major, 1890; Gliozzi *et al*., 1997).

Canis etruscus	*Leptobos etruscus*
Pachycrocuta brevriostris	*Procamptoceras brivatense*
Panthera gombaszoegensis	*Gallogoral meneghinii*
Felis lunensis	*Gazellospira torticornis*
Ursus etruscus	*Sus strozzi*
Mammuthus arvernensis	
Stephanorhinonus etruscus	
Equus stenonsis	
Eucaldoceros dicranios-ctenoides	
Pseudodama nestii	

36. Sites of the Upper Valdarno Basin (including Il Tasso and Faella), Arezzo, Tuscany, Italy (Tasso Faunal Unit). Mammalian fauna from the Upper Valdarno (Azzaroli *et al.,* 1988; Rook *et al.,* 2013).

Canis etruscus	*Leptobos etruscus*
Canis arnensis	*Leptobos vallisarni*
Canis falconeri	*Tapirus arvernensis*
Pachycrocuta brevirostris	*Eucladoceros*
Homotherium latidens	*Eucladoceros ctenoides*
Panthera gombaszoegensis	*Eucladoceros dicranios*
Acinonyx pardinensis	*Dama* sp.
Puma pardoides	*Cervus nestii*
Megantereon cultridens,	*Ovicaprine* sp
Ursus etruscus	*Sus strozzi*
Anancus arvernensis	*Macaca sylvana florentina*
Mammuthus meridionalis	*Mimomys savini*
Hippopotamus antiquus	
Stephanorhinus etruscus	
Equus stehlini	
Equus stenonis	

37. Untermassfeld, Thuringia, Germany. Mammalian fauna from Untermassfeld (Kahlke and Gaudzinski, 2005).

Canis mosbachensis	*Hippopotamus amphibius antiquus*
Canis (*Xenocyon*) *lycaonoides*	*Eucladoceros giulii*
Ursus cf *dolinensis* (= *U. rodei*)	*Cervus* s.l. *nestii vallonnetensis*
Meles hollitzeri	*Alces carnutorum*
Pachycrocuta brevirostris	*Capreolus cusanoides*
Homotherium crenatidens	*Bison menneri*
Megantereon cultridens adroveri	*Macaca sylvanus*
Lynx issiodorensis	*Hystrix* sp.

Puma pardoides	*Trogontherium cuvieri*
Acinonyx pardinensis pleistocaenicus	*Castor fiber*
Panthera onca gombaszoegensis	
Mammuthus sp.	
Equus wuesti	
Stephanorhinus etruscus	
Sus scrofa priscus	

38. Viatelle, Veneto, Italy. Mammal fauna of Viatelle (Bon *et al*., 1991).

Canis lupus aff *mosbachensis*	*Talpa* sp
Canis sp	*Lepus* cf *mediterraneus*
Vulpes alopcoides	*Lepus* sp
Ursus sp	*Allocricetus bursae*
Mustela nivalis	*Allocricetus* sp
Mustela putorius	*Cricetus cricetus praeglacialis*
Meles meles	*Cricetus* sp
Lutra lutra	*Mimomys reidi*
Panthera leo spelaea	*Mimomys savini*
Sus scrofa	*Mimomys* sp
Cervus cornaliai	*Clethrionomys* gr*. nageri*
Cervus elaphus	*Pliomys episcolpalis*
Cervus sp	*Arvicola praeceptor*
Dama somonensis	*Arvicola* sp
Megaloceros euryceros	*Allophaiomys ruffoi*
Capreolus capreolus pygargus	*Microtus agrestis*
Erinaceus sp	*Microtus arvalis*
Petenyia suavensis	*Microtus* cf *dentatus*
Sorex pachyodon	*Microtus subnivalis*
Beremendia fissidens	*Microtus* sp
Crocidura russula	*Pitymys (Microtus)* cf *faitoi*
Crocidura sp	*Pitymys (Microtus)* aff *savini*
Talpa cf *caeca*	*Pitymys (Microtus)* sp
Talpa europaea	*Apodemus sylvaticus*
Talpa romana	*Glis glis*

39. Voigtstedt, Thuringia, Germany. Mammalian fauna of Voigtstedt (Kahlke, 2002), carnivore species present (Thenius, 1965), small mammal fauna (Maul and Parfitt, 2010).

Canis mosbachensis	*Mimomys savini*
Ursus deningeri	*Microtus arvalinus*
Martes cf *martes*	*Microtus ratticepoides*
Mustela (putorius) cf *eversmanni*	*Apodemus flavicollis*
Meles meles cf *atavus*	*Erinaceus* cf*. europaeus*
Lutra simplicidens	*Desmana thermalis*
Felis sp	*Neomys newtoni*
Panthera cf *pardus*	*Macroneomys brachygnathus*
Bison schoetensacki	*Lepus* sp*.*
Mammuthus meridionalis	*Spermophilus dietrichi*
Mammuthus trogontherii	*Petauria helleri*

Stephanorhinus etruscus	*Castor fiber*
Equus sussenbornensis	*Trogontherium cuvieri*
Equus altidens	*Cricetus* sp.
Praemegaceros (=megaceroides) verticornis	*C. migratorius*
Alces latifrons	
Talpa europaea	
Talpa minor	
Sorex savini	
Sorex cf. *runtonensis*	
Clethrionomys cf. *hintonianus*	

40. Heppenloch, Baden-Wurttemberg, Germany. Mammalian fauna from Heppenloch (Adam, 1975; Kahlke *et al*., 2011).

Canis lupus	*Cervus elaphus*
Cuon alpinus fossilis	*Capreolus capreolus priscus*
Vulpes vulpes	*Crocidura* sp.
Ursus arctos	*Talpa gracilis*
Ursus spelaeus	*Talpa* cf. *praeglacialis*
Crocuta sp	*Talpa* cf. *episcopalis*
Felis sylvestris	*Myotis* sp.
Panthera leo	*Castor fiber*
Martes sp.	*Cricetus cricetus runtonensis*
Meles meles	*Cricetus cricetus praeglacialis*
Palaeoloxodon antiquus	*Clethrionomys* sp.
Equus steinheimensis	*Arvicola* cf *greenii*
Stephanorhinus hemitoechus	*Pitymys arvaloides*
Megaloceros sp.	*Pitymys gregaloides*
Dama sp.	*Microtus arvalinus*
Cervus elaphus	*Microtus ratticepoides*
Capreolus capreolus priscus	*Apodemus* sp.
Bos primigenius	*Macaca sylvana*
Bison priscus	*Homo* sp.
Bison cf *schoetensacki*	

41. Monte Zoppega I, Soave, Italy. Mammalian fauna from Monte Zoppega I (Bon *et al.,* 1991).

Canis mosbachensis	*Cervus elaphus*
Ursus spelaeus	*Cervus* cf. *Dama* cf *dama*
Felis cf. *Panthera leo spelaea*	*Megaceros (Megoloceros) euryceros*
Palaeoloxodon antiquus	*Capreolus capreolus*
Stephanorhinus hemitoechus	
Stephanorhinus kirchbergensis	
Hippopotamus amphibius	

42. Castello, Soave, Italy. Mammalian fauna of Castello (Bon *et al.,* 1991).

Canis lupus aff *mosbachensis*	*Pliomys* sp
Canis sp	*Arvicola* sp

Felis recce *Panthera leo spelaea*	*Allophaiomys ruffoi*
Panthera pardus cf *antiqua*	*Microtus arvalis*
Equus stenonis major	*Microtus* aff. *dentatus*
Cervus elaphus	*Microtus nivalis*
Cervus sp	*Microtus* cf. *nivalis*
Dama somonensis	*Microtus* cf. *nivaloides*
Capreolus capreolus	*Microtus subnivalis*
Crocidura zorzii	*Pitymys (*recce *Microtus)* cf. *fatioi*
Lepus europaeus	*Pitymys (*recce *Microtus)* aff. *subterraneus*
Lepus cf. *mediterraneus*	
Pliomys episcopalis	

43. Cengelle II, Soave, Italy. Mammalian fauna from Cengelle II (Bon *et al*., 1991).

Canis lupus	*Talpa caeca*
Vulpes vulpes	*Talpa europaea*
Vulpes sp.	*Talpa* cf. *europaea*
Ursus spelaeus	*Chiroptera indet.*
Mustela nivalis nivalis	*Lepus europaeus*
Mustela cf. *nivalis*	*Evotomys (Clethrionomys) sp.*
Meles meles	*Arvicola praeceptor*
Lutra lutra	*Arvicola* cf. *scherman*
Sus sp.	*Microtus agrestis*
Cervus sp.	*Microtus incertus*
Dama dama	*Microtus malei*
Dama sp.	*Microtus* sp
Capreolus capreolus	*Pitymys (Microtus)* cf. *fatioi*
Capra sp.	*Apodemus sylvaticus*
Sorex araneus tetragonurus	*Apodemus* sp.
Neomys fodiens	*Glis* sp.
Neomys sp.	

44. Weimar-Ehringsdorf, Germany. Mammalian fauna from the Lower and Upper Travertine (Kahlke, 2002).

Lower Travertine:	**Upper Travertine:**
Canis lupus	*Canis lupus*
Vulpes vulpes	*Ursus arctos*
Ursus arctos	*Ursus spelaeus*
Ursus spelaeus	*Panthera leo spelaea*
Lynx lynx	*Meles meles*
Bison priscus mediator	*Mustela* sp
Capreolus capreolus	*Martes martes*
Alces latifrons postremus	*Bison priscus*
Dama sp.	*Capreolus capreolus*
Megaloceros giganteus	*Alces latifrons postremus*
Cervus elaphus	*Megaloceros giganteus*
Sus scrofa	*Cervus elaphus*
Stephanorhinus kirchbergensis	*Mammuthus primigenius*
Stephanorhinus hemitoechus	*Coelodonta antiquitatis*

Equus taubachensis	*Stephanorhinus hemitoechus*
Palaeoloxodon antiquus	

45. Dobelhaldeschacht, Baden-Wurttemberg, Germany. Mammalian fauna from Dobelhaldeschacht (Ohmert, 1988; Rathgeber, 2008a, b).

Canis lupus	*Cervus elaphus*
Alopex cf. vulpes	*Capreolus capreolus*
Panthera leo spelaea	*Arvicola terrestris cantiana*
Ursus spelaeus	*Cricetus major*
Martes sp.	*Talpa europaea*
Mammuthus primigenius	*Lepus europaeus*
Equus sp	
Sus scrofa	

46. Taubach, Germany. Mammalian fauna at Taubach (Kahlke, 2002).

Canis lupus	*Dama dama*
Ursus arctos	*Megaloceros giganteus*
Ursus spelaeus	*Cervus elaphus*
Crocuta crocuta	*Sus scrofa*
Panthera leo cf *spelaea*	*Stephanorhinus kirchbergensis*
Bison priscus priscus	*Equus taubachensis*
Bison priscus mediator	*Palaeoloxodon antiquus*
Capreolus capreolus	*Castor fiber*
Alces latifrons postremus	

47. Bad Canstatt (Villa Seckendorf), Stuttgart, Germany. Mammal fauna of Bad Canstatt (Villa Seckendorf) (Ziegler, 1996).

Canis lupus	*Megaloceros giganteus*
Vulpes vulpes	*Cervus elaphas*
Ursus arctos	*Capreolus capreolus*
Ursus spelaeus	*Rangifer tarrandus*
Mustela putorius vel eversmanni	*Bos primigenius*
Crocuta crocuta spelaea	*Bison priscus cf mediator*
Panthera leo spelaea	*? Rupicapra rupicapra*
Mammuthus primigenius	*Dicrostonyx torquatus*
Coelodonta antiquatatis	*Lemmus lemmus*
Equus germanicus	*Arvicola terrestris*
Equus hydruntinus	

48. Hohle Fels, Ach Valley, Germany. Mammalian fauna present at Hohle Fels based on radiocarbon dated material analysed from the cave (Conard and Bolus, 2008).

Canis lupus	*Equus ferus*
Ursus spelaeus	*Rangifer tarandus*
Crocuta crocuta	
Mammuthus primigenius	

49. Kogelstein, Ach Valley, Germany. Mammalian fauna from Kogelstein (Munzel and Conard, 2004).

Canis lupus	*Megaloceros giganteus*
Vulpes vulpes,	*Rangifer tarandus*
Alopex lagopus	*Capra* sp.
Crocuta crocuta	*Rupicapra* sp.
Ursus spelaeus	*Marmota marmota*
Mammuthus primigenius	*Lepus* sp.
Equus ferus	
Bovidae sp.	

50. Perick Cave, Sauerland Karst, Germany. Mammalian fauna from the bone gravel from Perick Cave, separated into faunal types by Dietrich (2009).

1. mammoth steppe fauna:	**2. Intermediate fauna of taiga forest**
Alopex lagopus	*Canis lupus*
Gulo gulo	*Vulpes vulpes*
Equus ferus przewalskii	*Crocuta crocuta spelaea*
Equus hydruntinus	*Panthera leo spelaea*
Rangifer tarandus	*Ursus spelaeus*
Megaloceros giganteus	*Cervus elaphus*
Coelodonta antiquitatis	
Mammuthus primigenius	
Bison priscus	
Allocricetulus eversmanni	

51. Ranis (Ilsenhöhle), Thuringia, Germany. Mammalian fauna from the identified zones in Ranis (Muller-Beck and Workman, 1968).

Zones	**Mammalian fauna present**
Ranis 4: Leaf points, same age as Ranis 2.	*Rangifer tarrandus* *Ovibos moschatus* *Lepus timidus* *Alopex lagopus* *Ursus spelaeus* *Equus ferus* *Bos primigenius*
Ranis 3: Aurignacian level. No leaf points.	*Cervus elaphus* *Ursus spelaeus*
Ranis 2: LRJ (Lincombian-Ranisian-Jerzmanowician) leaf point assemblage (early upper Palaeolithic layer)	*Hyaena spelaea* *Cervus elaphus* *Ursus spelaeus* *Coelodonta antiquitatis*
Ranis 1: Mousterian, underlying mid Palaeolithic.	No fauna recorded

52. Grotta Paglicci, Puglia, Italy. Mammalian fauna present at Grotta Paglicci (Borgognini Tarli *et al.,* 1980; Delgado Huertas *et al*., 1997).

Canis lupus	*Microtus agrestis*
Cervus elaphus	*Microtus arvalis*
Equus caballus	*Apodemus sylvaticus*
Bos primigenius	*Homo* sp.
Capra ibex	
Rupicapra rupicapra	